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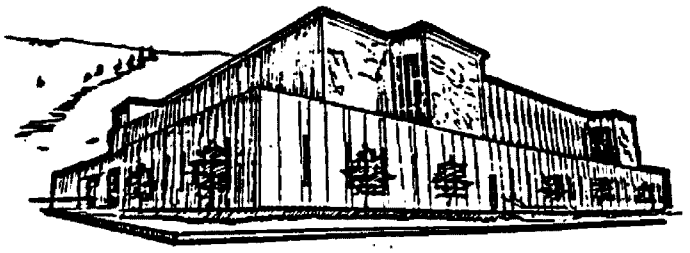

MORTALITY AND SEASONAL DISTRIBUTION OF WHITE-TAILED DEER IN AN AREA RECENTLY RECOLONIZED BY WOLVES

By

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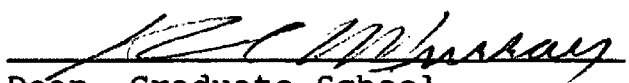

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Mortality and Seasonal Distribution of White-tailed Deer in an Area Recently Recolonized by Wolves (115 pp.)

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After an absence of 50 years, gray wolves (Canis lupus) began recolonizing northwestern Montana in the mid- 1980's. Wolf recolonization is controversial and the public has expressed concern about the potential impacts a wolf population may have on native ungulate populations. White-tailed deer (Odocoileus virginianus) are an important big game animal of hunters in northwestern Montana, and are also the major prey species of wolves. Between January 1990 and September 1991, I examined mortality and seasonal distribution of white-tailed deer in the North Fork drainage of the Flathead River in northwestern Montana and southeastern British Columbia. I also initiated an index to monitor deer population abundance over time, estimated the sex- and age- composition of the population, and examined habitat used by does during the fawning period.

Of 38 female white-tailed deer radio-collared during the study, wolves, bears (Ursus arctos and U. americanus), mountain lions (Felis concolor), coyotes (C. latrans), and humans each killed 2. Exact cause of death of 2 other deer could not be determined. Mean annual survival rate of marked females was 72.5%. Survival was highest during summer (100%) and autumn (94.9%), and lowest during spring (85.9%) and winter (89.0%). Deer congregated on 4 primary ranges during winter, and migrated an average of 11.7 km (Range = 0 - 40 km) to summer ranges that were scattered throughout the North Fork valley and up 3 side drainages. I initiated an index of pellet group counts that will permit biologists to detect a 20% change in deer population size with 90% certainty. Based on road-side surveys I conducted in 1990 and 1991, I estimated a spring herd composition of 24-29 Bucks : 100 Does, and 35-36 Fawns : 100 Does.

Does selected fawning areas that were at significantly lower elevations and closer to water than summer ranges. Fawning areas contained significantly fewer saplings, had less hiding cover between 1-2 m height (as viewed from 30.5 m), were more likely to occur in valley bottoms, and were more likely to contain edges than summer ranges. Deer also selected fawning and summer ranges differently based on distribution of canopy coverage of grasses and trees larger than pole-size, and distribution of vegetation structural class.

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I owe special thanks to my committee chairman Dr. Dan Pletscher. In spite of being the busiest and most dedicated man I have ever met, Dan always managed to be a readily available source of wisdom, good advice, encouragement, humor, and friendship. Without his dedication and determination, this study would not have happened. Thanks Dan.

Committee member Dr. Les Marcum always took time to express his concern during all aspects of the study, and constantly reminded me of the importance of safety. Without him, I'm sure I would have set off for the field more than once without warm socks or would have been otherwise unprepared for nasty weather. Other committee members Drs. Bob Ream, and Andy Sheldon provided valuable logistic support, advice, and editorial comments on this thesis. Dr. Joe Ball also offered comments and suggestions during the early stages of the writing process. Dr. Hans Zuuring

offered statistical advise during several stages of my data analysis, and Virginia Johnston efficiently and accurately handled all clerical responsibilities associated with this research project.

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Lori Oberhofer, Jerry Altermatt, and Mike Lahti assisted with the study for several months and performed reliably and admirably during the usually arduous, and always intensive, task of habitat analysis. Barbara and Mike Bureau located study animals, and otherwise "took care of my deer" during my absence from the North Fork.

Glacier National Park Rangers Regi Altop, Scott Emmerich, Kyle Johnson, and Roger Semler assisted with

mortality investigations in "the Park", and cooperated with all aspects of the study. Dave Hoerner and the pilots of Eagle Aviation flew skillfully during all telemetry flights. John and Pat Elliott, Ray Hart, Tom Ladenburg, and Tom Reynolds graciously permitted me to sample habitat on their private land.

I would also like to thank my friends and graduate colleagues past and present. None of you could refrain from reminding me that "wildlifers" are supposed to be a jocular bunch, and not just a bunch of uptight, old fuddy-duddies. You made me laugh often. Thank you.

Finally, I would like to make a 3-fold dedication of this thesis:

To my parents who always trusted and believed in me. I appreciate their love, encouragement, and financial support more than I could ever adequately express.

To Lori Oberhofer. Her friendship, companionship, love, and encouragement made my graduate career pass by quickly, and made all tasks seem less severe.

To the memory of Kevin Roy. Kevin was lost in October 1991 when his plane failed to return from a routine telemetry flight for radio-collared grizzly bears in Wyoming. Kevin was one of the first people I met when I arrived in Missoula. He immediately impressed me, not only with his friendliness, but with his ethics and concern for all animals. Kevin was a fellow graduate student and

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CHAPTER 1

MORTALITY AND SEASONAL DISTRIBUTION OF WHITE-TAILED DEER IN AN AREA RECENTLY RECOLONIZED BY WOLVES

INTRODUCTION

Although the gray wolf (Canis lupus) was once common throughout the western United States, it was extirpated from the Northern Rocky Mountains by widespread public and private control efforts. Reported sightings of wolves were extremely rare in Montana by the 1930's, and remained sporadic through the late 1970's (Day 1981). Occasional sightings were probably of dispersing or lone wolves. No documented cases of wolf reproduction in the western U.S. occurred until 1986 when a den was found in Glacier National Park (Ream et al. 1987, 1989, 1991). Another den was found in Glacier Park in 1987, and 2 dens were located in British Columbia within 10 km of the international border in 1988. Wolves denned within Glacier National Park again in 1989, but the litter failed. In 1990 wolves denned at 2 sites in Glacier National Park and produced 12 pups. By September 1991, 3 wolf packs (25 wolves) were known to inhabit the western portion of Glacier National Park and maintain ranges that extend into the immediate surrounding areas of the

Flathead National Forest and southeastern British Columbia.

The on-going natural recolonization of wolves in northwestern Montana has occurred in an area unlike many other areas where wolf studies have been conducted. Because this area has been without a breeding population of wolves for >50 years, ungulate populations in Glacier National Park had probably reached an equilibrium with their habitat and other predators. Additionally, prey diversity in this area is higher than in most other systems studied. Most studies of wolf-prey interactions have been conducted in areas with only 1 or 2 primary prey species (e.g. Murie 1944, Mech 1966, Messier and Crete 1985, Ballard et al. 1987). White-tailed deer (Odocoileus virginianus), mule deer (O. hemionus), elk (Cervus elaphus), and moose (Alces alces), are relatively abundant and provide a potential prey base for wolves in northwestern Montana. At higher elevations, low numbers of mountain goats (Oreamnos americanus) and bighorn sheep (Ovis canadensis) are also present.

Wolf recolonization is highly controversial. Researchers studying public attitudes toward wolves have documented a concern for native ungulate populations (e.g. Kellert 1985, McNaught 1987, Bath 1987, Bath and Buchanan 1989, Tucker and Pletscher 1989). To answer questions from the public, resource managers require reliable information on impacts of wolf predation on the ungulate populations they manage.

In the North Fork drainage of the Flathead River in northwestern Montana from 1985-1991, more than half (60%) of the prey killed by wolves were white-tailed deer (Boyd et al. in prep.). Although white-tailed deer are the top management priority of the Montana Department of Fish, Wildlife and Parks in northwestern Montana, cause-specific mortality rates and seasonal movement patterns of deer in this area were unknown.

Results of a predator-prey study in an area being recolonized by wolves may yield valuable information with applications to other areas where wolves may recolonize or be reintroduced. My research objectives were to:

1) Evaluate cause-specific mortality of white-tailed deer within the area recolonized by wolves;

2) Document seasonal distribution of white-tailed deer, including identification of key areas of seasonal use;

3) Initiate an index to monitor deer abundance over time; and,

4) Estimate population sex- and age- structure.

STUDY AREA

This research was conducted in the valley of the North Fork of the Flathead River in northwestern Montana and southeastern British Columbia. The study area encompassed the range occupied by wolves in Glacier National Park, and extended from Camas Creek in Glacier National Park northward

to 30 km beyond the Canadian border (Fig. 1.1).

The North Fork valley was formed in the early Tertiary period when a gap opened behind a massive slab of Precambrian sedimentary rock that slid eastward on the Lewis Overthrust Fault (Alt and Hyndman 1973). Pleistocene glaciers further sculpted the valley and left behind the moraines that resulted in the rolling topography present today (Alt and Hyndman 1973). The valley bottom varies from 4-10 km in width and rises from 1,024 m elevation in the south to 1,375 m in the northern part of the study area. Peaks of the Whitefish Range form the western border of the valley, and the Livingston Range defines the eastern border.

Land east of the North Fork of the Flathead River lies in Glacier National Park. West of the river, land is a mosaic of Flathead National Forest, state forest, and private property. During the study, female deer residing outside Glacier National Park were vulnerable to hunting during the archery season from 1 September to 14 October 1990, and during the first 2 weeks of the regular 5 week big game season from 21 October to 25 November 1990. In British Columbia, land on both sides of the river is primarily under provincial ownership, and in 1990 white-tailed deer of either sex could be harvested by hunters from 1 September to 9 September during the archery season, or during the regular big game season from 10 September through 30 November.

The climate of this area is transitional between a

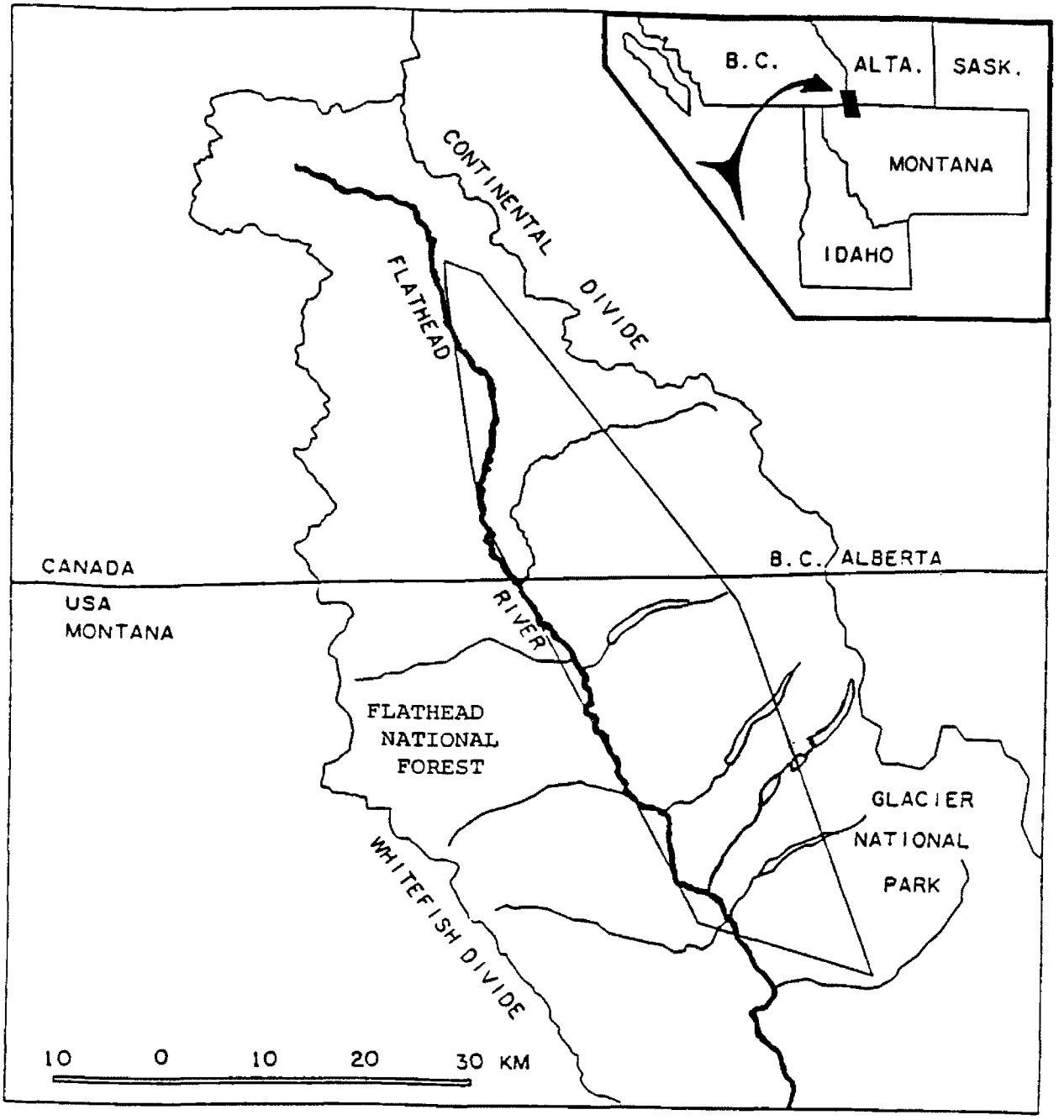


Fig. 1.1. Study area in the North Fork drainage of the Flathead River, and the approximate area populated by wolves in 1990 and 1991 in Glacier National Park and the surrounding areas of Flathead National Forest and southeastern British Columbia. Only ranges of wolves that potentially affected radio-collared deer are included in the figure.

northern Pacific coastal type and a continental type (Finklin 1986). Mean temperature ranges from -9 C in January to 16 C in July (Singer 1979). Snow normally covers the study area from mid-November through mid-April. Between 1 December and 31 March during the 30 year period between 1951 and 1980, rangers at the Polebridge Ranger Station reported an average maximum daily snow depth of 65.4 cm (Finklin 1986).

Dense lodgepole pine (Pinus contorta) forests dominate most of the North Fork valley, but sub-alpine fir (Abies lasiocarpa), spruce (Picea spp.), western larch (Larix occidentalis), and Douglas-fir (Pseudotsuga menziesii) communities exist throughout the valley. Abundant meadows and riparian areas are dispersed within the study area. Detailed descriptions of vegetative communities in this area have been provided by Habeck (1970), Jenkins (1985), and Krahmer (1989).

METHODS

Trapping

I selected 4 white-tailed deer wintering areas in Glacier National Park for trapping: 1) the Sullivan Meadow area, 2) Bowman Road, 3) Kintla Lake, and 4) the North Fork of the Flathead River bottom near the confluence with Kintla Creek. These 4 winter ranges provided a northern, central, and southern sample of deer within the area inhabited by

wolves. Deer were trapped on the Kintla Lake, Sullivan Meadow, and Bowman Road winter ranges from 21 January through 31 March 1990, and from 26 November 1990 to 26 February 1991. I trapped deer along the river bottom near the confluence of Kintla Creek only during the latter trapping period.

Deer were trapped with modified, elk-sized Clover traps (described by Thompson et al. 1989) or standard Clover traps (Clover 1956). All traps were baited with alfalfa hay (certified to be free of noxious weeds). Female white-tailed deer were manually restrained (Appendix A) and instrumented with a radio transmitter (MOD-500, Telonics, Inc., Mesa, Ariz.) with a mortality sensor (4-hr delay). Radio collars were colored with permanent black and brown marking pens to make them as inconspicuous as possible. When does >1 yr old were captured, I administered 0.75-1.00 cc Lidocaine hydrochloride (local anesthetic) into gum tissue surrounding the root of a canine tooth. After induction of the local anesthetic, I removed the tooth. Deer were released following tooth extraction. Teeth were sent to Matson's Lab (Milltown, Mont.) for age-determination via cementum analysis. Male white-tailed deer and all mule deer were released without being handled.

Mortality

I tried to monitor activity signals of all radio-collared deer at least once daily. When a radio signal

indicated that a deer had not moved in >4 hours, I carefully approached the animal on the ground and performed a post-mortem examination to determine cause of death (O'Gara 1978, Wobeser and Spraker 1980). During mortality investigations, I took numerous precautions to avoid encountering feeding predators (primarily grizzly bears--see Appendix B). When predation occurred, I recorded kill and chase information, and when possible, attempted to establish the pre-mortality condition of the animal by analysis of femur marrow, kidney fat index, and description of other vital organs (Thorne et al. 1982). If near-total consumption of the carcass made it impossible to ascertain if the deer was killed or was scavenged soon after death, I attributed cause of death to what I considered the most likely scenario and labeled the death either due to "probable" predation or unknown causes.

I used methods described by Heisey and Fuller (1985) and computer software MICROMORT (version 1.3, Heisey 1987) to calculate seasonal and annual survival and cause-specific mortality rates based on "radio-days" per interval. Survival rates from February to September 1990 were compared to survival rates from the same period during 1991 (Z test, 2-tailed). I pooled data from both years into months, then further pooled monthly categories into 4 intervals I felt best reflected weather patterns and most significant biological periods for deer. December, January, February, and March were considered "winter" months because there was

usually a substantial amount of snow on the ground throughout this period. April, May, and June were pooled into the "spring" category. Spring months encompassed migration from wintering areas to summer ranges, and included the fawning period. July and August were considered "summer" months, and September, October, and November were grouped into the "autumn" interval. Migration from summer ranges to winter ranges occurred mostly during the autumn interval. Females were legal game for hunters during archery season and for 2 weeks of the regular big game season west of the river during this interval. I compared the average daily survival rates between seasons (Z test, 2-tailed), and considered differences between seasonal daily rates to be significant at $P \leq 0.03$ (Bonferroni correction for multiple comparisons [Kleinbaum et al. 1988:32] necessitates a critical value at $P \leq 0.03$ to yield overall $\alpha = 0.10$ for 3 seasonal comparisons). Because of sample size limitations, I did not attempt to calculate age-specific mortality rates.

To compute annual survival and cause-specific mortality rates and 95% confidence limits, I first considered lost radio signals to be independent of mortality, then considered lost signals as mortalities on the day following the last active signal (Heisey and Fuller 1985:673). During the study, 2 transmitters apparently failed. One radio began transmitting a mortality signal while the deer was

known to be alive and active. The transmitter remained in mortality mode until the signal was lost completely 2 weeks later. This transmitter was considered a malfunction and was excluded from survival and mortality rate calculations after the last signal.

Seasonal Distribution

To identify key areas of seasonal use and document movement patterns, I attempted to locate all deer weekly by triangulating at least 3 strong radio bearings. I plotted radio bearings on USGS (1:24,000) or Energy, Mines and Resources Canada (1:50,000) topographic maps, and selected a location either at the center of the smallest triangle defined by 3 or more signal azimuths, or at the intersection of 2 such triangles. I divided locations into 6 categories of precision (<1 ha, 1-3 ha, 3-6 ha, 6-12 ha, 12-25 ha, or >25 ha) based on size of the triangle or polygon. Variable topography and lack of an extensive road network within the study area frequently inhibited my ability to get close-range, line-of-sight signal fixes. Consequently, precise triangulations were often difficult to obtain. Trial radio azimuths (n = 59) to transmitters at known locations yielded an average angular error of 9.5° (SD = 7.6). To reduce error associated with imprecise telemetry azimuths in calculation of seasonal ranges, I included only locations in which the area of the triangle or polygon defined by the intersection of ≥3 signal azimuths was <25 ha. If I could

not locate deer from the ground, I located them from a Cessna 180 or 182 airplane when possible.

I computed minimum convex polygon and 95% harmonic mean (25 grid cell) range for winter and summer ranges of each radio-collared deer (McPAAL ver. 1.2, Stuwe and Blohowiak nd.). To estimate migration distances, I calculated the straight-line distance between the approximate center of each deer's winter and summer range.

Index of Population Abundance

Based on field work conducted during spring 1986 and 1987, Tucker (1991) concluded that an annual count of pellet groups was the most feasible method for monitoring white-tailed deer population trend in the North Fork area. Tucker (1991) stressed that any method of evaluating population trend must be undertaken for several consecutive years before trend results are considered certain. Because of the importance of yearly replication, it was imperative that the sampling scheme could be conducted with a reasonable amount of effort and manpower. Without these considerations, it is unlikely that the monitoring effort would be continued in the future. Tucker (1991) reported that it should be possible to detect a 20% change in the white-tailed deer population with 90% confidence if a reasonable amount of effort was expended.

Following Tucker's (1991) recommendations, I initiated a pellet-group sampling scheme in spring 1990. Concurrent

with the disappearance of snow in late April, I counted pellet groups in 80 uncleared, 1.8 m-radius plots on 11 pairs of transects (n = 880 plots). Transects were initiated at various 1.6 km intervals (all distances to starting point of transects were measured in miles with a vehicle odometer) along the Inside North Fork Road (Glacier Route 7). Transects were distributed to encompass the entire range of habitat types and geographic variation in the area. I assessed variability from the 1990 sampling effort and used the sample size formula of Neff (1968:603) to determine the sample size necessary to detect a 20% change in the index with 90% certainty.

I refined the location of transects in 1991 to avoid crossing or by-passing creeks or large areas of standing water during the spring runoff period. In addition, I made an effort to locate transects at intervals that would increase the ease of replication in subsequent years.

Pellet groups were counted in plots along 13 pairs of parallel transects (n = 1,040 plots) from 3 May to 24 May 1991. Pairs of 2 km transects were spaced at various 1.6 km intervals along the Inside North Fork Road (Glacier route seven) from the Polebridge Ranger Station north toward Kintla Lake, and from the Polebridge Ranger Station south to 1.6 km south of Anaconda Creek. Five transect pairs were located north of Polebridge; 8 pairs were located south of Polebridge (Table 1.1).

Table 1.1. Location of unmarked pellet transects along Inside North Fork Road (Glacier Route 7) in Glacier National Park, surveyed Spring 1991.

Transect	Location of Transect Pairs
North1	1 mile (1.6 km) north of Polebridge Ranger Station. Transect begins at bridge over creek north of Akokala Creek.
North2	0.3 miles (0.5 km) north of south end of Round Prairie.
North3	0.5 miles (0.8 km) north of Ford Creek patrol cabin.
North4	1.5 miles (2.4 km) north of Ford Creek patrol cabin.
North5	2.5 miles (4.0 km) north of Ford Creek patrol cabin.
South1	1 mile (1.6 km) south of Polebridge Ranger Station.
South2	2 miles (3.2 km) south of Polebridge Ranger Station.
South3	3 miles (4.8 km) south of Polebridge Ranger Station.
South4	4 miles (6.4 km) south of Polebridge Ranger Station.
South5	6 miles (9.7 km) south of Polebridge Ranger Station. 50 m south of entrance to Quartz Creek campground.
South6	7 miles (11.3 km) south of Polebridge Ranger Station. 1 mile (1.6 km) south of Quartz Creek campground.
South7	South end Anaconda Creek bridge.
South8	1 mile (1.6 km) south of south end of Anaconda Creek bridge. Begin transect 100 m north of road (road runs east-west here).

I used the same techniques to count pellets in both 1990 and 1991. Seven pairs of transects surveyed in 1991 were the same as transects surveyed in 1990. All transects originated from the Inside North Fork Road and ran due east. Plots were spaced at 50 m intervals along transects (40 plots per transect). Upon reaching the end of a transect, observers paced 200 m south, then counted pellets in plots along a transect in the opposite direction (due west) and parallel to the first transect.

Only pellet groups lying within a plot and containing >20 pellets were counted. If a group of pellets was intersected by the perimeter of the plot, the portion of the group within the plot was estimated to the nearest 10%. Age of each pellet group was categorized as "new", "intermediate" (probably deposited during previous winter), or "old" (defecated before previous winter) based on subjective characteristics. Pellets that were shiny, sticky, and moist were considered new; pellets that were not shiny, but were dark and dry were grouped into the intermediate age category; and pellets that were white, or very dry and crumbly were considered old.

Pellets labeled as old were not considered in the analysis. I combined new and intermediate aged pellet groups and computed the number of groups per transect, mean number of groups per plot per transect, total number of groups counted, mean number of groups per total plots, and

the variance among all plots sampled. The presence of a large number of zero values resulted in a highly skewed distribution that I was unable to transform to approximate normality, and consequently necessitated the use of non-parametric methods for comparative analysis. Use of non-parametric tests instead of a paired Student's t-test resulted in a sacrifice of power that required a 6% greater sample size to achieve the desired level of precision (Hettmansperger 1984:164). I used the Kruskal-Wallis test to test for differences in variances among transects, and the Mann-Whitney U test to compare results from the 7 transects that were sampled in both 1990 and 1991.

Population Sex- and Age- structure

During spring green-up, large numbers of white-tailed deer gather in fields along the North Fork Road to take advantage of the new grass and forb shoots. One hour before sunset, from mid-April to mid-May, 1990 and 1991, I drove from 1.6 km south of Coal Creek (mile marker 24) to Polebridge (mile marker 32) and searched for deer. All deer were counted and observed with 10x binoculars. If possible, deer were classified as adult (>1 yr-old) males or females, or fawns (<1 yr-old). I used the Mann-Whitney U test to compare nightly count totals between years. Age distribution was estimated from deer killed by hunters and checked through the big game check station at Canyon Creek (16 km south of Camas Creek on the North Fork Road) in 1989

and 1990. I used the age structure of the 1989 and 1990 hunter harvest to construct a life table (Caughley 1977) for does, and compared the average annual survival rate to the annual survival rate of my radio-collared sample. Female age structure was compared between years, and to the age structure of radio-collared study animals (Kolmogorov-Smirnov test, 2-tailed).

RESULTS

Trapping

From January through March 1990, 50 white-tailed deer and 11 mule deer were captured. Twenty-three female white-tailed deer were fitted with radio collars (Appendix C). During winter 1990-1991, 54 white-tailed deer were captured and 15 females were radio-collared (Appendix C). Nine deer were captured and radio-collared on the Kintla Lake winter range, 10 were radio-collared on the Kintla Creek/North Fork Flathead River bottom wintering area, 6 on the Polebridge/Bowman Creek wintering area, and 13 were radioed on the Sullivan Meadow winter range. Three deer died during the trapping procedure. One broke its neck in a fall during release from the trap and had to be euthanized. Two others died during handling, apparently from stress-related trauma. A radio collar was removed from 1 deer (#128) after it became known that it was habituated to humans and was being fed regularly.

Mortality

Between 21 January 1990 and 6 September 1991, 12 radio-collared deer died. Wolves, bears (1 grizzly [Ursus arctos] and 1 probably black [Ursus americanus]), mountain lions (Felis concolor), coyotes (Canis latrans), and humans each killed 2 radio-collared deer (Table 1.2). One was killed by an unknown predator, and cause of death of another could not be determined (Table 1.2). Non-human predators killed 4 radio-collared deer during winter and 6 during spring months, but killed none during summer or autumn (Table 1.2). Humans were responsible for the death of 1 radio-collared deer in June. This deer was habituated to people and had been acting aggressively toward Glacier Park visitors at the Kintla Lake Campground. Glacier Park officials elected to attempt to relocate the deer out of the area, but the deer was injured during the capture attempt and had to be euthanized. Another radio-collared deer was killed by a hunter during the fall hunting season in British Columbia.

Mortalities were almost evenly distributed among age classes (Table 1.2), but non-human-related causes resulted in the death of 33% (1) of radio-collared fawns (< 1 yr.), and 20% (5) of prime-aged (1.5 - 6.5 yrs.) does, (Appendix C). Forty-four percent (4) of old (>6.5 yrs.) radio-collared deer were killed by non-human causes (Table 1.2, Appendix C).

Survival rate estimates for the period 1 February - 31

Table 1.2. Cause-specific mortality of radio-collared female white-tailed deer in the North Fork drainage of the Flathead River, 21 January 1990 - 6 September 1991.

ID#	Cause	Predator	Date	Age (yrs)
122	Predation	Wolves	03/13/90	2.8
117	Probable Predation	Wolves	06/04/90	10.0
106	Probable Predation	Bear	06/13/90	14.0
105	Accident[1]	Human	06/26/90	7.0
109	Hunting	Human	11/05/90	6.4
130	Predation	Mountain Lion	01/31/91	4.6
135	Predation	Coyote	02/13/91	0.7
137	Predation	Mountain Lion	03/24/91	10.8
108	Predation	Unknown[2]	04/10/91	2.8
107	Predation	Coyote	04/17/91	5.8
124	Predation	Grizzly bear	04/28/91	1.9
113	Unknown		05/27/91	8.0

1 Killed by accident during translocation attempt in Glacier National Park.

2 Predation occurred during snowstorm that obliterated much of the evidence. Only a small portion of carcass remained.

August 1990 (S = 0.804, 95% CL = 0.649 - 0.996) and the corresponding period in 1991 (S = 0.791, 95% CL = 0.655 - 0.954) were not significantly different (Z = 0.11, 2-tailed; P = 0.91). Annual estimated survival rate based on pooled data from the period 21 January 1990 through 6 September 1991 was 0.725 (95% CL = 0.599 - 0.877)(Table 1.3), but decreased to 0.704 (95% CL = 0.577 - 0.859) if the 1 lost radio signal was considered a mortality (Table 1.4). Survival was highest during summer (S = 100%) and autumn (S = 94.9%, 95% CL = 85.5% - 100.0%), and lowest during spring (S = 85.9%, 95% CL = 76.7% - 96.1%) and winter (S = 89.0%, 95% CL = 79.3% - 99.8%) months (Table 1.3).

Survival during winter was not significantly different from survival during spring (Z = 0.89, 2-tailed; P = 0.373), but winter survival was almost significantly less (Z = -2.00, 2-tailed; P = 0.046 [Bonferroni correction for multiple comparisons--differences significant at $P \leq 0.03$]) than survival during summer. Winter survival was not different from fall survival (Z = -0.51, 2-tailed; P = 0.610). Survival during spring was significantly less than survival during summer (Z = -2.65, 2-tailed; P = 0.008), but the spring survival rate was not significantly different than survival during autumn (Z = -1.27, 2-tailed; P = 0.204). Summer and autumn survival estimates were not significantly different (Z = 1.00, 2-tailed; P = 0.317). Mortality rate estimates for all non-human-related causes

Table 1.3. Daily survival during seasons, seasonal and annual survival rates (S), and number of mortalities (M) of radio-collared white-tailed deer, 21 January 1990 - 6 September 1991.

				Seasonal Survival				Daily Survival during Seasons			
						95% C.L.				95% C.L.	
Season	Days/ Season	Radio-days /Season	M	S	Variance	Lower	Upper	S	Variance	Lower	Upper
Winter (Dec-Mar)	121	4,142	4	0.890	2.700E-03	0.793	0.998	0.9990	2.325E-07	0.9981	1.0000
Spring (Apr-Jun)	91	4,179	7	0.859	2.444E-03	0.767	0.961	0.9983	3.988E-07	0.9971	0.9996
Summer (Jul-Aug)	62	2,528	0	1.000	0.000E+00	1.000	1.000	1.0000	0.000E+00	1.0000	1.0000
Autumn (Sep-Nov)	91	1,722	1	0.949	2.511E-03	0.855	1.000	0.9994	3.367E-07	0.9983	1.0000
		Annual Rate:		0.725	4.998E-03	0.599	0.877				

Table 1.4. Daily survival during seasons, seasonal and annual survival rates (S), and number of mortalities (M) of radio-collared white-tailed deer (considering 1 lost radio signal as a mortality from unknown cause on day following last active signal), 21 January 1990 - 6 September 1991.

				Seasonal Survival				Daily Survival during Seasons			
						95% C.L.				95% C.L.	
Season	Days/ Season	Radio-days /Season	M	S	Variance	Lower	Upper	S	Variance	Lower	Upper
Winter (Dec-Mar)	121	4,141	5	0.864	3.184E-03	0.760	0.982	0.9977	2.905E-07	0.9977	0.9999
Spring (Apr-Jun)	91	4,179	7	0.859	2.444E-03	0.767	0.961	0.9983	3.988E-07	0.9971	0.9996
Summer (Jul-Aug)	62	2,528	0	1.000	0.000E+00	1.000	1.000	1.0000	0.000E+00	1.0000	1.0000
Autumn (Sep-Nov)	91	1,722	1	0.949	2.511E-03	0.855	1.000	0.9994	3.367E-07	0.9983	1.0000
		Annual Rate:		0.704	5.137E-03	0.577	0.859				

were higher in winter and spring than in summer or autumn.

Annual cause-specific mortality rates ranged from 3.6% (bears) to 5.7% (humans), but 95% confidence limits for all mortality sources overlapped significantly (Table 1.5). Mountain lion predation attributed to an annual deer mortality rate of 5.5%, while wolves and coyotes were each responsible for 4.6% (Table 1.5) of the annual mortality rate. Annual mortality from all known non-human-related causes was 18.2% (95% CL = 6.7% - 29.7%). Three of 9 deer killed by predators were killed on the periphery of their winter range or during migration from winter to summer range.

Mortalities were normally investigated on the day following the first received mortality signal (mortalities were considered to have occurred on the day prior to the day during which first mortality signal was received) (n = 10, median = 2 days after death; H_L = 1, H_U = 3.25). On average, carcasses (n = 10) had been >80% consumed when I arrived to begin the examination. Kidneys were absent from all deer killed by predators. I collected femurs from 7 predator-killed carcasses. Femur marrow fat content ranged from 7.6% to 79.8% (n = 6, $\overline{X}$ = 41.7%, SD = 29.5); fat content of marrow from 1 femur was not measured, but the marrow was very soft and partially gelatinous.

Seasonal Distribution

Radio-collared white-tailed deer wintered in 4 major

Table 1.5. Annual cause-specific mortality rates of radio-collared white-tailed deer, 21 January 1990 - 6 September 1991.

Cause of Death	Annual Mortality Rate	Variance	95% C.L. Lower	95% C.L. Upper
Wolf	0.046	1.028E-03	0.000	0.108
Bear	0.036	6.230E-04	0.000	0.085
Mountain Lion	0.055	1.434E-03	0.000	0.129
Coyote	0.046	1.028E-03	0.000	0.108
Human	0.057	1.770E-03	0.000	0.140
Unknown	0.036	6.230E-04	0.000	0.085

areas within the range inhabited by wolves in western Glacier National Park: the Kintla Lake area, the Kintla Creek/North Fork River bottom area, the Polebridge/Bowman Lake area, and the Sullivan Meadow area (Fig. 1.2). From early April to early June (Table 1.6), females migrated 0 - 40 km ($\bar{x}$ = 11.7 km, SD = 10.7) (Table 1.7) from winter ranges to summer ranges (Fig. 1.3). Deer migrated in all directions between seasonal ranges, but more traveled north to summer range (n = 16) than south (n = 4). Of 23 deer wintering in Glacier National Park, 14 (61%) migrated to summer ranges outside Glacier Park borders (Fig. 1.3). Two of 7 (29%) deer that wintered outside Glacier Park migrated to summer ranges within park boundaries (Fig. 1.3). Five of 21 (24%) radio-collared deer were non-migratory in 1990, and 4 of 25 (16%) radio-collared deer did not migrate seasonally in 1991 (Tables 1.6-1.7).

Deer typically returned to the same general seasonal range each year. However, 3 collared deer migrated in 1 year but not in the other (#'s 101 and 110 did not migrate in 1990, but did migrate in 1991; #111 migrated in 1990, but did not migrate in 1991). In summer 1991 one collared deer (#103) traveled between its 1990 summer range and a new range 4.5 km away several times.

Most deer arrived on summer ranges between mid-April and mid-June (Table 1.6). Summer ranges of most radio collared deer were in the main valley of the North Fork of

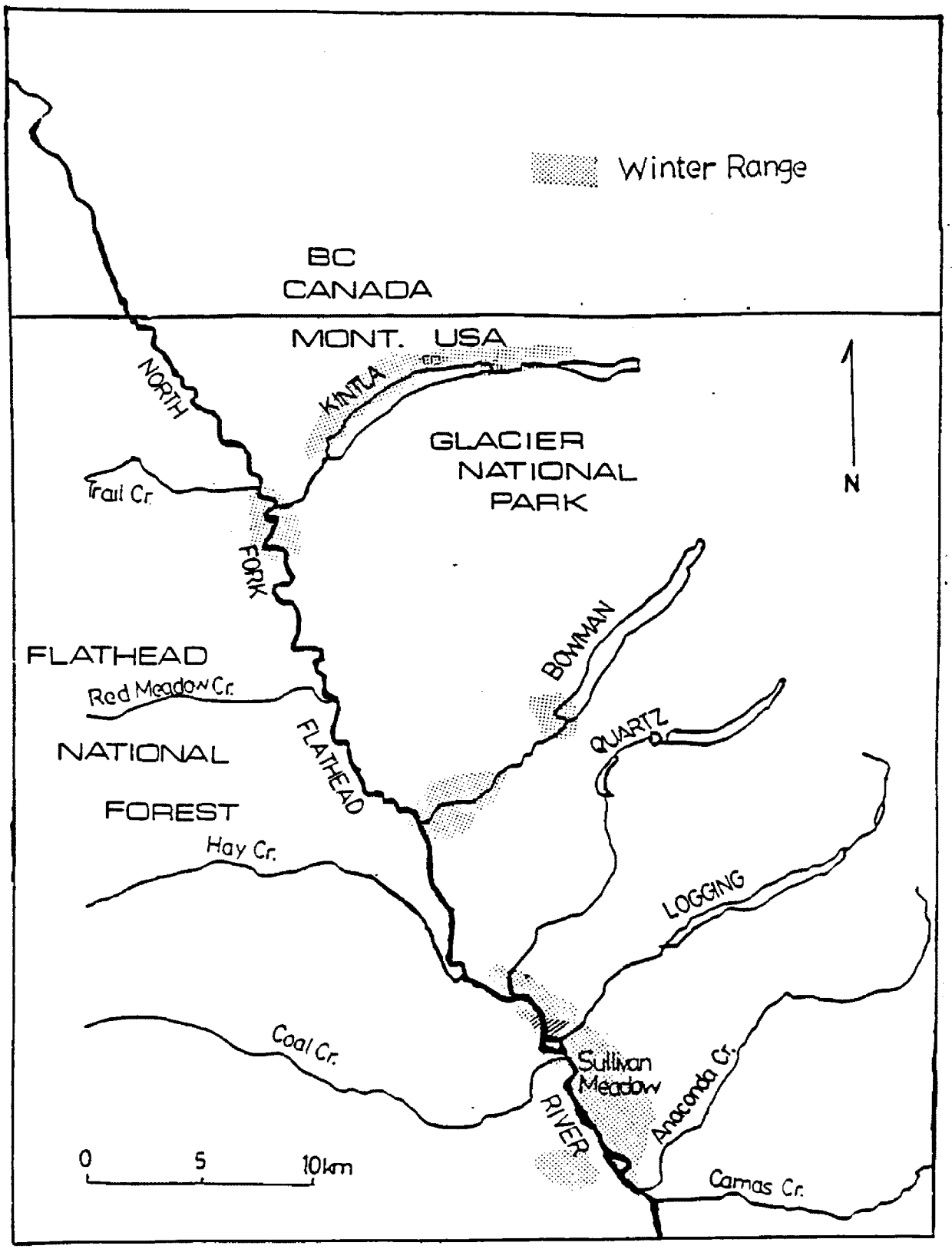


Fig. 1.2. Winter ranges of radio-collared white-tailed deer in the North Fork drainage of the Flathead River in northwestern Montana.

Table 1.6. Dates of migration to seasonal ranges of radio-collared female white-tailed deer in the North Fork of the Flathead River Drainage, 1990-1991.

ID#	Depart from Winter Range	Arrive on Summer Range	Depart from Summer Range	Arrive on Winter Range
101	06/03/91	06/04/91	Did not migrate in 1990	
102	04/22/91	04/26/91	12/04/90	12/05/90
103	04/28/91	05/01/91	09/27/90	12/12/90
104	Radio Failure			
105	Did not migrate		Mortality	
106	Early April	Mid May '90	Mortality	
107	04/18/90	Mid May '90	09/01/90	11/11/91
108	Mid April	05/07/90	09/03/90	Late Dec.
109	Mid April	Mid April	09/27/90	Mortality
110	04/29/91	05/05/91	Late January	02/04/91
111	06/07/90	06/08/90	06/30/90	07/07/90
112	04/12/91	04/13/91	12/05/90	Late Jan.
113	04/27/91	05/08/91	Early Sept.	12/12/91
114	Did not migrate		Did not migrate	
115	Did not migrate		Did not migrate	
116	Mid April	Mid April	Early Jan.	Early Jan.
117	04/01/90	04/11/91	Mortality	
118	05/08/91	05/22/91	10/03/90	10/16/90
119	Late March	Late March	Mid Dec.	Mid Dec.
120	Mid April	04/17/91	12/12/90	12/13/90
121	05/01/91	05/15/91	08/24/90	12/13/90
122	Mortality			
123	Mid April	Mid May		12/13/90
124	04/14/91	04/15/91		12/20/90
125	05/16/91	Unknown[1]		10/10/91
126	05/07/91	05/16/91		
127	06/06/91	06/07/91		
128	Radio collar removed			
129	04/30/91	05/01/91		12/20/90
130	Mortality			
131	Early June	Mid June		
132	05/12/91	05/16/91		
133	04/26/91	05/01/91		
134	Did not migrate			
135	Mortality			
136	Late May	Late May		
137	Mortality			
138	05/17/91	05/21/91		

1 Date of arrival on summer range unknown; radio signal was last heard on 05/16/91. #125 returned to its Polebridge area winter range on 10/10/91.

Table 1.7. Seasonal distribution and migration distances (km) of white-tailed deer radio-collared winter 1989-1990 and winter 1990-1991.

ID#	Winter Range	Summer Range	Migration Distance
101	Kintla Lake, GNP[1]	Starvation Cr., GNP[2]	3
102	Kintla Lake, GNP	Colts Cr., Pvt[3]	11
103	Kintla Lake, GNP	Couldrey, Cr., BC[4]	21
105	Kintla Lake, GNP	Kintla Lake, GNP	0
106	Kintla Lake, GNP	Ford Cr., GNP	5
107	Kintla Lake, GNP	Harvey Cr., BC	40
108	Kintla Lake, GNP	8 km S. Polebridge, Pvt	27
109	Kintla Lake, GNP	Couldrey Cr., BC	21
110	Confl. Camas Cr., FNF[5]	Polebridge, GNP	18
111	Sullivan Meadow, GNP	Dutch Creek, GNP	8
112	Sullivan Meadow, GNP	Big Prairie, GNP	16
113	Sullivan Meadow, GNP	Mid. Quartz Lake, GNP	14
114	Sullivan Meadow, GNP	Sullivan Meadow, GNP	0
115	Sullivan Meadow, GNP	Sullivan Meadow, GNP	0
116	Sullivan Meadow, GNP	Sullivan Meadow, GNP	1
117	Sullivan Meadow, GNP	Mud Lake, GNP	7
118	Sullivan Meadow, GNP	Hay Creek, FNF	23
119	Sullivan Meadow, GNP	Logging Cr., GNP	3
120	Sullivan Meadow, GNP	Hidden Meadow, GNP	7
121	Sullivan Meadow, GNP	Tepee Lake, FNF	31
123	Sullivan Meadow, GNP	Anaconda Creek, GNP	16
124	Quartz Creek, GNP	Unknown - mortality	
125	Polebridge, GNP	Unknown - lost signal	
126	Bowman Rd., GNP	2 km S. Procter Lk., BC	30
127	2 km S. Kintla Cr.[6], Pvt	Confluence Sage Cr., GNP	12
128	2 km S. Kintla Cr., Pvt	Unknown - collar removed[7]	
129	Sullivan Meadow, GNP	Polebridge, GNP	14
130	Unknown[8]	Unknown - mortality	
131	1 km S. Kintla Cr., FNF	Whale Cr., FNF	5
132	2 km S. Kintla Cr., Pvt	Tepee Cr., FNF	7
133	Kintla Cr., FNF	2 km NE Sage Cr.[9], GNP	10
134	Kintla Cr., FNF	1 km S Kintla Cr., FNF	0
135	2 km S. Kintla Cr., Pvt	Unknown - mortality	
136	Ford Work Center, FNF	1 km N Ford Work Ctr., FNF	1
137	Kintla Cr., Pvt	Unknown - mortality	
138	Kintla Cr., Pvt	4 km N BC Customs, BC	17

1 GNP = Glacier National Park.
2 1990 at Kintla Lake; 1991 at confluence N. Fork/Starvation Cr.
3 Pvt = Private property.
4 BC = British Columbia.
5 FNF = Flathead National Forest.
6 Kintla Cr. refers to Kintla Cr./North Fork confluence.
7 Unknown. Collar removed from human-habituated deer.
8 Unknown. Spent early winter near Polebridge, but was killed 5 km South in mid-January.
9 2 km Northeast of North Fork/Sage Cr. confluence.

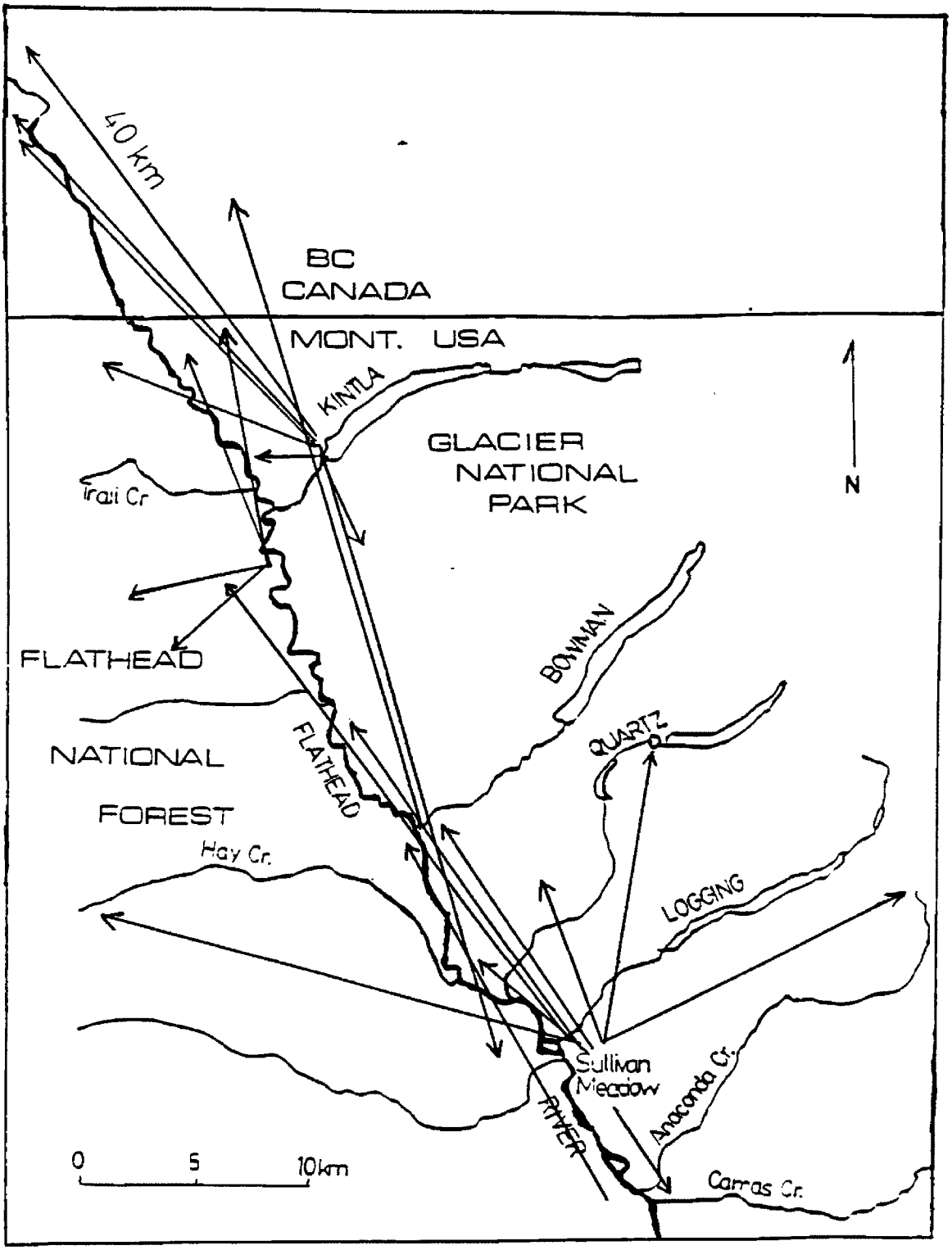


Fig. 1.3. Direction radio-collared female white-tailed deer traveled from winter ranges to summer ranges in the North Fork drainage of the Flathead River.

the Flathead River; only 3 spent summers up side drainages (Fig. 1.4).

Deer began migrating from summer ranges as early as 24 August and arrived on winter ranges as early as 16 October (Table 1.6). One deer (#111) returned from its summer range in early July (Table 1.6), but this movement was probably associated with the loss of a fawn. Most deer (57%) migrated from their summer ranges by early October, but 43% remained on their summer ranges until early December or later (Table 1.6). Of the 14 deer that migrated from summer ranges to winter ranges in 1990, 6 (43%) occupied intermediate "transitional" ranges for >1 month.

Only 5 of 18 (28%) radio-collared deer were outside the sanctuary of Glacier National Park during the regular fall hunting season in 1990. Of these, 3 ranged exclusively in areas either close to occupied houses where it was unlikely that they would be shot, or on land posted against hunting.

Winter ranges (95% harmonic mean) of radio-collared deer were smaller (median = 107 ha; H_L = 63.0, H_U = 193.5) than summer ranges (median = 162 ha; H_L = 92.5, H_U = 208.0) (Table 1.8), but the size difference was not statistically significant (ln transformation; $\underline{t}$ = 1.134, df = 25, $\underline{P}$ = 0.268). Minimum Convex Polygon winter ranges were not significantly larger (median = 213 ha; H_L = 130.0, H_U = 400.5) than Minimum Convex Polygon summer ranges (median = 156 ha; H_L = 94.5, H_U = 299.5) (ln transformation; $\underline{t}$ =

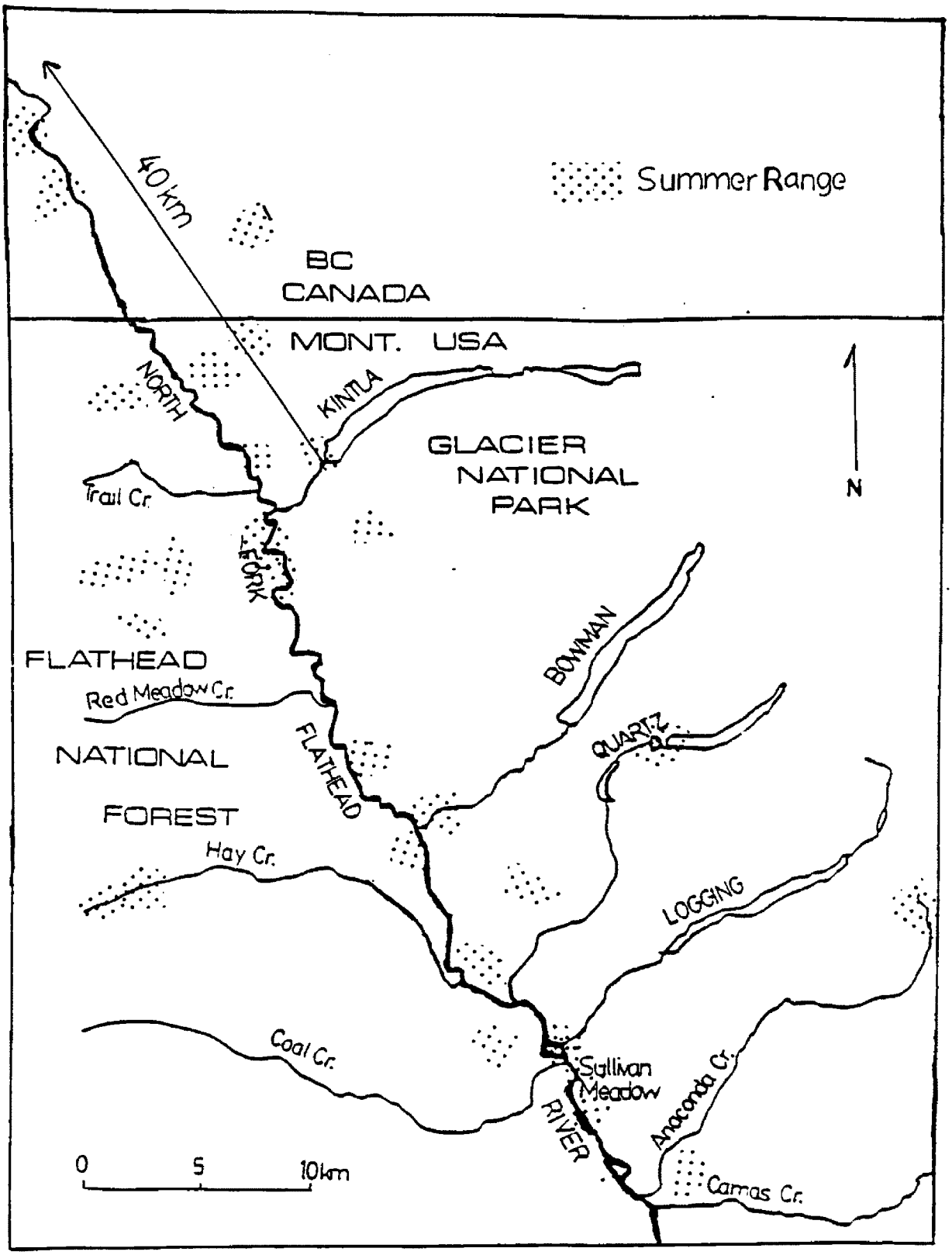


Fig. 1.4. Summer ranges of radio-collared white-tailed deer in the North Fork drainage of the Flathead River in northwestern Montana and southeastern British Columbia.

Table 1.8. Minimum convex polygon (MCP) and 95% harmonic mean size of winter[1] and summer[2] ranges of radio-collared female white-tailed deer (N = number of locations with "error polygon" <25 ha used to calculate seasonal range).

	Winter Range (ha)			Summer Range (ha)		
ID#	N	MCP	95% harmonic	N	MCP	95% harmonic
101	8	950	189	10	400	226
102	7	1,096	1,064	28	314	207
103	8	127	89	20	642	526
107	10	487	429	10	46	87
108	7	847	319	34	82	108
109				16	41	70
110	11	1,519	638	29	185	253
111	12	293	173	30	156	178
112	6	420	77	31	374	207
113	10	120	74	5	13	23
114	9	150	99	30	216	162
115	11	262	143	29	285	162
116	9	354	34	30	281	420
118	9	309	29	24	75	139
119	8	176	79	35	170	209
120	7	213	62	7	14	29
121	11	381	192	28	107	140
123	9	1,594	126	5	91	71
124	8	1,205	363			
125	8	121	195			
126	9	303	107	8	638	192
127	10	200	143	7	151	41
128	8	317	229			
129	11	205	110	30	121	158
131	7	107	44	5	3,631	98
132	8	144	202	25	1,417	1,092
133	9	102	64	8	117	85
134	9	139	77	28	98	131
135	5	133	59			
136	9	74	46	29	128	175
137	6	22	30			
138	7	40	62	22	281	331

1 Winter 1990-1991.

2 For marked deer alive in both summer 1990 and 1991, data are reported for the year in which the greatest number of locations were obtained. If an equal number of locations were obtained in both summers, the larger home range sizes are reported.

1.266; df = 25, $\underline{P}$ = 0.217). In most cases, seasonal range sizes estimated by 95% harmonic mean and Minimum Convex Polygon methods were similar; however, in several instances, Minimum Convex Polygon estimates were substantially larger than the harmonic mean estimate (Table 1.8). In these cases, if a collared deer traveled a large distance between 2 or more areas without spending time in between, the 95% harmonic mean method resulted in separate, exclusive ranges for each of the areas, whereas, the Minimum Convex Polygon method connected the outermost points of each area and computed the area within the large polygon. Minimum Convex Polygon estimates were not significantly larger than 95% harmonic mean estimates for summer ranges (ln transformation; $\underline{t}$ = 0.850, df = 26, $\underline{P}$ = 0.403), but Minimum Convex Polygon estimates for winter ranges were different than winter range sizes computed by 95 % harmonic mean methods (ln transformation; $\underline{t}$ = 5.346, df = 30, $\underline{P}$ < 0.001).

Index of Population of Abundance

In April and May 1990, 451.1 new and intermediate aged deer pellet groups were counted in 880 plots ($\overline{x}$ = 0.513 groups per plot, SD = 1.017, Range = 0 - 7.0) on 11 pairs of transects. Transect locations were modified in 1991, and 310.5 pellet groups were counted in 1040 plots on 13 pairs of transects ($\overline{x}$ = 0.299 groups per plot, SD = 0.738, Range = 0 - 6.8) (Table 1.9). Difference in variability among transects was significant (Kruskal-Wallis H = 135.73, 12 df,

Table 1.9. Number of pellet groups per transect and mean number of groups per plot in pellet transect pairs surveyed during spring 1991.

Transect	# Plots	Groups / transect	$\bar{x}$ / plot	SD	Range
North1	80	20.8	0.260	0.668	0 - 4.0
North2	80	10.0	0.125	0.460	0 - 3.0
North3	80	9.0	0.113	0.356	0 - 2.0
North4	80	10.1	0.126	0.369	0 - 2.0
North5	80	17.3	0.216	0.539	0 - 2.0
South1	80	2.0	0.025	0.157	0 - 1.0
South2	80	1.0	0.013	0.112	0 - 1.0
South3	80	27.8	0.348	0.632	0 - 2.5
South4	80	22.1	0.276	0.688	0 - 3.0
South5	80	74.9	0.936	1.396	0 - 6.8
South6	80	59.6	0.745	1.130	0 - 5.8
South7	80	27.3	0.341	0.707	0 - 3.0
South8	80	28.6	0.358	0.662	0 - 2.7
Total = 1040		310.5	0.299	0.738	0 - 6.8

$P < 0.001$). Transects South5 and South6 were located on a deer winter range south of Quartz Creek. Significantly more pellet groups were counted on plots in these 2 transects than in all others (Table 1.9) (Wilcoxon Sign Rank, 2-tailed; $P < 0.02$). I counted significantly fewer pellet groups on transects South1 and South2 compared to all other transects (Wilcoxon Sign Rank, 2-tailed; $P \leq 0.074$). Although few new and intermediate aged pellet groups were counted in plots on transects South1 and South2 (Table 1.9), several old groups were counted in the plots, and new and intermediate aged groups were observed outside the plots. Based on results of all transects, a sample size of at least 413 plots is required to detect a 20% change in the deer population with 90% certainty (sample size based on power of Student's t-test and normally distributed data--a 6% larger sample size [>438] is required for skewed distributions compared with a Mann-Whitney U test).

Seven of 13 transect pairs sampled in 1991 were the same as transects sampled in 1990. In the 560 plots on these 7 transect pairs, significantly more pellet groups were counted in 1990 ($\tilde{x} = 0.413$, SD = 0.895, Range = 0 - 7.0) than in 1991 ($\tilde{x} = 0.277$, SD = 0.742, Range = 0 - 6.8) (Mann-Whitney, 2-tailed; $U = 170{,}051$, $n_1 = 560$, $n_2 = 560$; $P = 0.001$).

Population Sex- and Age- Structure

I counted 1,172 white-tailed deer in 11 evenings from

20 April to 8 May 1990 ($\bar{x}$ = 106.5 deer/evening, SD = 29.1) (Table 1.10). Of the deer I was able to categorize, 102 were adult males (14.9%), 429 were adult females (62.5%), and 155 were fawns (<1 yr-old) (22.6%); 486 deer could not be classified. Counts in 1990 yielded ratios of 24 bucks : 100 does, and 36 fawns : 100 does. In 10 evenings between 26 April and 15 May 1991, I counted 1,296 white- tailed deer ($\underline{x}$ = 129.6, SD = 16.0) (Table 1.11). Adult males comprised 17.4% (n = 113) of the classified sample, while females comprised 61.1% (n = 397), and fawns made up 21.5% (n = 140) of the sample (Table 1.11). Ratios for 1991 counts were 29 bucks : 100 does, and 35 fawns : 100 does.

Number of deer classified as males, females, and fawns were not different between years (Mann-Whitney, 2-tailed; $\underline{P}$ > 0.60). More deer were unclassified in 1991 than in 1990 (Mann-Whitney, 2-tailed; $\underline{U}$ = 17, n_1 = 11, n_2 = 10; $\underline{P}$ = 0.007), and total number of deer counted per evening was significantly greater in 1991 than in 1990 (Mann-Whitney, 2-tailed; $\underline{U}$ = 28, n_1 = 11, n_2 = 10; $\underline{P}$ = 0.057).

During the 1989 regular hunting season, hunters checked 51 bucks through the big game check station. Results from cementum analysis of teeth pulled from checked animals indicated 14 1.5 yr.-olds, 19 2.5 yr.-olds, 7 3.5 yr.-olds, 7 4.5 yr.-olds, 2 5.5 yr.-olds, 1 6.5 yr.-old, and 1 8.5 yr.-old made up the male deer harvest. In 1990 hunters harvested 55 bucks, including 1 fawn, 17 yearlings, 16 2.5

Table 1.10. Results of spring road-side counts of white-tailed deer, 20 April - 8 May 1990.

Date	Males	Females	Fawns	Unknown	Total
04/20/90	7	37	7	44	95
04/22/90	15	32	10	44	101
04/24/90	13	31	18	34	96
04/25/90	11	54	12	71	148
04/30/90	9	56	15	62	142
05/01/90	14	59	20	58	151
05/04/90	7	33	13	44	97
05/05/90	5	25	15	35	80
05/06/90	14	58	21	23	116
05/07/90	0	27	17	22	66
05/08/90	7	17	7	49	80
Totals	102	429	155	486	1,172

Table 1.11. Results of spring road-side counts of white-tailed deer, 26 April 1991 - 15 May 1991.

Date	Males	Females	Fawns	Unknown	Total
04/26/91	6	38	10	62	116
04/28/91	6	24	11	69	110
04/29/91	4	50	16	65	135
05/01/91	8	25	4	82	119
05/02/91	10	38	8	64	120
05/03/91	19	48	20	41	128
05/07/91	13	42	18	69	142
05/10/91	17	31	13	73	134
05/12/91	22	62	28	54	166
05/15/91	8	39	12	67	126
Totals	113	397	140	646	1,296

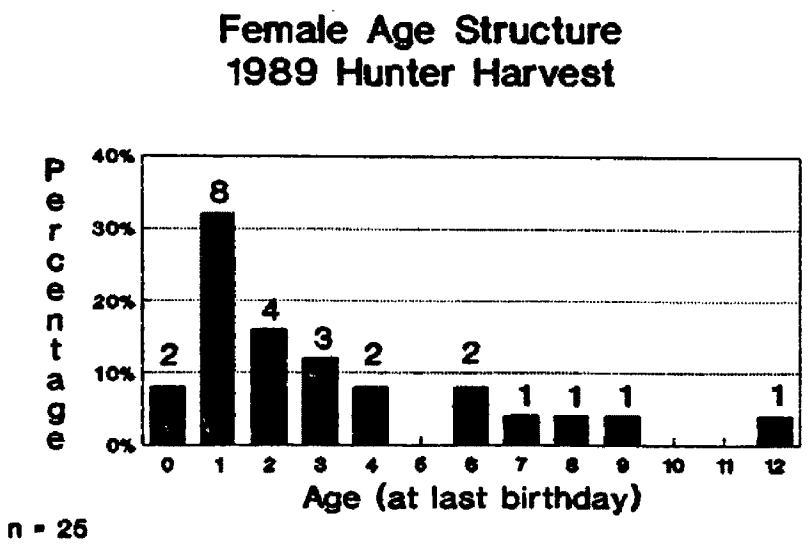
yr.-olds, 14 3.5 yr.-olds, 3 4.5 yr.-olds, 1 6.5 yr.-olds, 2 7.5 yr.-olds, and 1 8.5 yr.-olds. Hunters harvested 25 female white-tails in both 1989 and 1990 (Fig. 1.5). Analysis of a life table (Caughley 1977) based on the age-structure of combined 1989 and 1990 doe harvests (Fig. 1.6) yielded an average annual survival rate of 68.5% (combined across all age classes).

Age distribution of female white-tails in the 1989 and 1990 hunter harvests did not differ between years (Kolmogorov-Smirnov, 2-tailed; $\underline{P} = 0.494$). Age-structure of the radio-collared sample (Appendix C) (Fig. 1.7) did not differ significantly from the age-structure of does harvested in 1989 and 1990 (Fig. 1.6) (Kolmogorov-Smirnov, 2-tailed; $\underline{P} = 0.236$), and I believe my radio-collared sample was representative of the population.

DISCUSSION

Mortality

Wolves are the major predator of white-tailed deer throughout the deer's historic range (Mech 1984), but few areas where their ranges overlap today have predator-prey systems as complex as the predator-prey system in the North Fork drainage. Unlike predator-prey systems in most areas, wolves in the North Fork valley prey on deer, elk, and moose, but must compete with humans and high densities of mountain lions, grizzly and black bears, and coyotes.



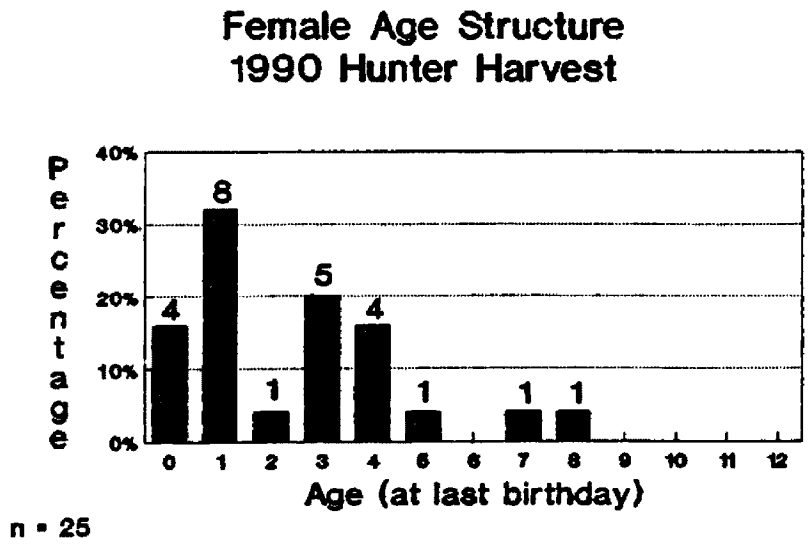


Fig. 1.5. Age distribution of female white-tailed deer killed by hunters during 1989 and 1990 seasons.

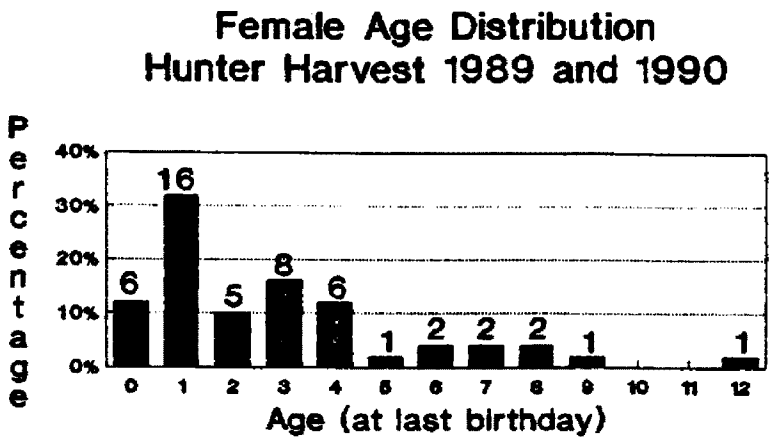


Fig. 1.6. Age distribution of female white-tailed deer in combined hunter harvest during 1989 and 1990.

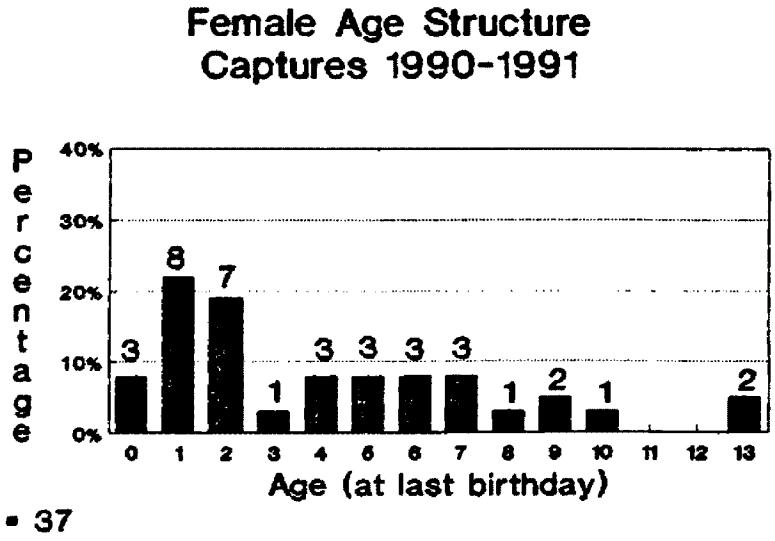


Fig. 1.7. Age distribution of female white-tailed deer captured and radio-collared in 1990 and 1991.

Researchers in other areas where wolves are the primary predator of deer report annual survival rates similar to the rates I calculated in this study (S = 0.704 - 0.725). When I used the survival rate formula presented by Heisey and Fuller (1985) to estimate annual survival of deer studied by Hoskinson and Mech (1976), I calculated an annual rate of 0.682 (both sexes and all age classes combined). Similarly, data presented by Nelson and Mech (1981) yielded an annual survival estimate of 0.674 for all white-tails when calculated by the techniques of Heisey and Fuller (1985). But, when fawns (6-12 months) were eliminated from the calculation, annual survival was much higher (S = 0.779) (Nelson and Mech 1981). Nelson and Mech (1986a) reported an annual survival rate of 79.0% (95% CL = 0.72 - 0.87) for adult (≥2 yrs.) female white-tailed deer in Minnesota. Annual survival of yearling females was similar (S = 0.80) to adults, but fawn survival was only 0.31 (Nelson and Mech 1986a). Fuller (1990) reported an annual survival rate of 0.69 for adult (≥1 year) female white-tails (95% CL = 0.62 - 0.77).

Researchers who studied deer in areas without wolves also reported annual survival rates similar to those estimated in this study. Dusek et al. (1989) calculated an annual survival rate of 78% for female white-tails ≥ 1 yr.-old in eastern Montana. Fifty percent of fawns, however, died before reaching their first birthday (Dusek et al.

1989). Annual survival of adult (≥ 2 years) female white-tails in an intensively farmed area in Illinois was 71.4%, while survival of yearling females was 62.4% (Nixon et al. 1991). Annual survival rates of 70% for adult females were also reported by Eberhardt (1969).

Although my survival estimates were similar to survival estimates for white-tailed deer in other areas inhabited by wolves, annual wolf-induced mortality was typically higher in studies conducted in Minnesota. Nelson and Mech (1986a) reported a wolf-induced mortality rate for adult female white-tails of 17% per year, and Hoskinson and Mech (1976) reported an annual wolf-induced mortality rate of 22.5% (both sexes and all age classes included in calculation). Additionally, Nelson and Mech (1981) reported that wolves were responsible for ≥ 45% of all white-tailed deer mortality. In contrast, Fuller (1990) reported a wolf-induced annual mortality rate (M = 0.036) of female white-tails similar to the rate I estimated.

White-tailed deer are hunted intensively throughout their range. Consequently, hunting typically results in a major proportion of annual mortality. Fuller (1990) and Nixon et al. (1991) reported hunting-related mortality rates of 22.3% and 21.3%, respectively for adult female white-tails. Dusek et al. (1989) indicated that hunting was responsible for 81% of all mortality of adult white-tails in eastern Montana. Hunting-related mortality in my study was

much lower. In the North Fork area, many deer arrived on wintering areas in the security of Glacier National Park before the regular hunting season opened outside the park. Others resided on private property where hunting was prohibited, and thus were protected.

Most authors reported lowest survival of adult females during autumn when hunting seasons resulted in high mortality (Dusek et al. 1989, Fuller 1990, Nixon et al. 1991). Non-human-related mortality is typically highest during winter and spring (Mech 1975, Nelson and Mech 1986a, Dusek et al. 1989, Fuller 1990, Nixon et al. 1991). As was the case in my study, most authors reported highest survival during summer (Nelson and Mech 1981, 1986a; Dusek et al. 1989; Fuller 1990; Nixon et al. 1991). High survival of adult deer during summer may be the result of wolves and other predators preying heavily on fawns (Pimlott 1967, Van Ballenberghe et al. 1975, Voight et al. 1976, Fritts and Mech 1981, Mech 1984, Nelson and Mech 1986a, Fuller 1989). In the North Fork drainage, survival in autumn is undoubtedly enhanced by the security from hunting provided by Glacier National Park and private land closed to hunting in the valley bottom.

Deer are most vulnerable to predation during winter when movements are restricted by deep snow (Nelson and Mech 1986b) and their physical condition may be poor (Blouch 1984, Mattfield 1984). When snow conditions are severe,

wolves may kill and feed at an increased rate, but fail to consume carcasses to the extent they would under other conditions (Mech 1966, Kolenosky 1972, Mech 1975). Although deer may be in prime physical condition at the onset of winter, after a long, harsh winter, a doe's physical reserves may be depleted (Mattfield 1984). In the absence of high quality browse required to meet energy requirements of pregnant females, does may sacrifice bone and body tissue to nourish fetuses (Verme and Ullrey 1984). As a result, the condition of a pregnant doe may continue to deteriorate through parturition. Severe winter weather during this study, and the resultant poor physical condition of deer, likely contributed to predation and the resultant higher spring mortality rate.

Because marrow is the last fat deposit to be used as nutritional condition deteriorates (Harris 1945), fat content in femur marrow is often used to indicate pre-death condition of ungulates. Some researchers have regarded femur marrow fat as an indicator of body fat content, but Mech and Delgiudice (1985) cautioned that an animal with any depletion of marrow fat is in poor condition. Under this interpretation, all deer killed by predators during my study were suffering from malnutrition.

Under certain circumstances (e.g., combination of severe winter weather, degradation of habitat, over-hunting, and high predation), wolves, and presumably other predators,

can regulate ungulate numbers (Pimlott 1967, Mech and Karns 1977, Gasaway et al. 1983, Bergerud and Ballard 1988). Ungulates and their predators probably evolved in relatively stable environments that could not support prey populations of high density (Pimlott 1967). Mech and Karns (1977) reported a case in which declining habitat and several consecutive severe winters decreased deer populations to the point that predation by wolves was enough to suppress deer population growth and maintain the deer population at low numbers. Presence of alternate prey species may sustain high wolf populations while deer numbers decline, and permit wolves to exert unusually high predation pressure on a declining deer population (Mech and Karns 1977).

Pimlott (1967) and Mech and Karns (1977) emphasized that the greatest influence wolves may have on deer populations is through predation on fawns. Severe winter weather with lack of sufficient nutritious browse results in decreased production of fawns and increased neo-natal mortality (Verme 1969). Depending on relative densities of deer and their predators, intensive predation on fawns could substantially impact deer numbers (Pimlott 1967, Mech and Karns 1977, Mech 1984). However, Mech and Karns (1977) stressed that deer populations are very resilient and only under the combined effects of declining habitat, several consecutive severe winters, and intensive predation pressure are populations unable to survive.

Although wolves and other predators may greatly impact deer populations in areas where habitat is diminishing, diversity of habitat and human habitat alterations permit deer to thrive at high numbers (Pimlott 1967, Mech and Karns 1977) and it is unlikely that predators can exert a significant influence on high-density ungulate populations (Pimlott 1967, Mech and Karns 1977). Habitat in the North Fork drainage is diverse. The recent Red Bench Fire (1988), cyclic pine beetle (Dendroctonus ponderosae) infestations of conifers, and development and habitat alterations west of Glacier National Park have created a dynamic and diverse habitat that improves the likelihood that white-tailed deer populations will continue to thrive at high numbers.

Results presented in this study provide a strong base of information on mortality patterns of white-tailed deer in the area; however, annual and seasonal survival can vary greatly, especially in areas like the North Fork that have highly variable winter snow depths. It would be premature to form solid conclusions on the impact of predation on the white-tailed deer population based on only 20 months of field data. Research on mortality of ungulates in the North Fork area will continue beyond completion of this study. Long term information on ungulate mortality should be carefully evaluated prior to making conclusions regarding annual or seasonal survival, or cause-specific mortality rates presented in this thesis.

Seasonal Distribution

In the northern and mountainous parts of their distribution, white-tailed deer may migrate long distances seasonally to use habitat that will optimize their survival and reproduction (Marchington and Hirth 1984, Smith and Coggin 1984). Migration distance between seasonal ranges in this study were consistent with distances reported by other researchers (Rongstad and Tester 1969, Verme 1973, Hoskinson and Mech 1976, Slott 1980, Mundinger 1981, Nelson and Mech 1981, Krahmer 1989, Nixon et al. 1991).

Several authors have reported that migration of deer from winter range to summer range occurs when snowpack decreases enough to permit them to travel freely (Severinghaus and Cheatum 1956, Rongstad and Tester 1969, Verme 1973, Hoskinson and Mech 1976, Nelson and Mech 1981, Krahmer 1989). In my study, most instrumented deer departed winter ranges in early- to mid- April concurrent with decrease in snow pack, but others remained on winter ranges until early June, long after snow had disappeared. Late departure from winter range suggests that factors other than dissipation of snowpack are involved in triggering spring migration. Deer migrated in all directions from winter ranges, but most deer traveled north, and only a few traveled up eastern or western side drainages. Deer studied in the North Fork area by Krahmer (1989) tended to migrate east from their winter range at Big Creek. The apparent

preference of deer to remain in the main valley bottom may be associated with higher habitat diversity in these areas (Slott 1980, Nelson and Mech 1981, Leach 1982, Krahmer 1989). Regardless of direction of migration, deer most often traveled along water courses, trails, or roadways when enroute to seasonal ranges (pers. obs., radio-tracking data).

White-tailed deer migrate from their summer ranges to areas at lower elevations and with greater thermal cover to escape the extremes of winter (Marchington and Hirth 1984, Smith and Coggin 1984). These autumn or early winter migrations to winter range are triggered by drops in temperature (Ozoga and Gysel 1972, Hoskinson and Mech 1976, Nelson and Mech 1981) or accumulation of snow (Hoskinson and Mech 1976, Nelson and Mech 1981). Temperature appeared to be important in initiating migration along the North Fork, but several deer migrated to fall ranges, intermediate between summer and winter ranges, and remained for several weeks. Although some deer migrated from fall ranges to winter ranges prior to the first snowfall, others remained on fall ranges after snow had accumulated. This behavior suggests that while temperature changes or weather fronts may be instrumental in initiating migration from summer range, snow accumulation is probably the factor most influential in determining when deer arrive on winter range. It is also possible that late departure from fall ranges may

be associated with females coming into estrous during November.

Summer Range.--An individual or group of white-tailed deer will occupy almost the same summer range each year (Leach 1982, Ozoga et al. 1982, Marchington and Hirth 1984, Krahmer 1989). Prior to giving birth, matriarchal does become solitary (Nelson and Mech 1981) and return to, and defend the same fawning grounds each year (Ozoga et al. 1982). This retention of traditional fawning areas for family groups may serve to enhance reproductive success during times of high population density (Ozoga et al. 1982). Fidelity to summer ranges may also act to increase familiarity with food sources and escape routes within a home range, and thus, increase survival of both does and their fawns (Leach 1982). In my study, most deer that were monitored during both summers used almost the same summer range each year. However, 3 deer migrated in 1 year but not the other. These cases of infidelity to summer ranges may have been related to maternal relationships, pregnancy status, or loss of a fawn. If a matriarchal female is not pregnant, she is not likely to chase off a daughter from a previous year, and the 2 deer may summer together. In subsequent years, if either or both of the 2 deer are pregnant, the younger is likely to be driven off (Ozoga et al. 1982) to find its own fawning area in a different area than the previous year. If a doe isolates herself during

the fawning period but subsequently loses her fawn(s), she may rejoin her family group (Ozoga et al. 1982).

Summer range sizes reported in my study are similar to those reported by other investigators (Kohn and Mooty 1971, Hoskinson and Mech 1976, Slott 1980, Nelson and Mech 1981, Leach 1982, Krahmer 1989, Nixon et al. 1991). Several deer, however, exhibited unusually large home ranges. One yearling (#131) was apparently chased off by its mother (#134) during the fawning period. The yearling ranged widely before radio contact was lost several weeks later. Another deer (#132) exhibited restricted movements characteristic of a parturient female (Ozoga et al. 1982, Huegel et al. 1985) in mid-June, but apparently lost her fawn and wandered extensively afterwards. Ozoga et al. (1982) reported a similar incident. Small minimum convex polygon and harmonic mean summer ranges (<50 ha) reported for the North Fork area in my study may be the result of a small number of locations rather than restricted movements of a radio-collared deer.

Winter Range.--Snow depth and temperature may have a substantial influence on both the home range size of deer, and on how the habitat is used (Rongstad and Tester 1969). Singer (1979) reported that snow depth was the key factor determining habitat partitioning among ungulates in the North Fork valley, and noted that deer spent severe winters in mature spruce stands and other areas where overstory was

dense. Because deer can move more easily beneath trees where snow depth is less than in the open, closed-canopy, mature forests are used to provide cover during harsh winters or when snow depth is >45 cm (Peek 1984). Krahmer (1989) concluded that deer winter ranges in the North Fork valley were located at lower elevations, had more edge and canopy cover than random areas, and were generally located in mature bottomland forest communities that provided shelter in close proximity to small openings.

Sizes of winter ranges in my study were similar to those reported by Krahmer (1989), but several deer exhibited much larger winter ranges. I observed several unusual movements throughout the winter that undoubtedly contributed to the large sizes of winter ranges used by several deer. On at least 1 occasion, 2 deer (#102 and #108) traveled >8 km from their winter range near the foot of Kintla Lake to the foot of Upper Kintla Lake. Deer #110 traveled 18 km from its Polebridge area winter range to an area near the confluence of Camas Creek and the North Fork in early February. Deer #123 and #124 also moved about extensively between Sullivan Meadow and Quartz Creek (up to 9 km) during the winter.

Index of Population Abundance

Counts of ungulate pellet groups have been used extensively since the 1930's to monitor big game numbers, population trend, and distribution (Neff 1968; Freddy and

Bowden 1983a, 1983b; Tucker 1991). Permanently marked sampling plots have been recommended over temporary unmarked plots because of the inherent variability added by unmarked plots (Neff 1968; Freddy and Bowden 1983a, 1983b). Temporary plots typically vary slightly in location each year, and add the difficulty of differentiation between new and old pellet groups (Neff 1968; Freddy and Bowden 1983a, 1983b). However, temporary plots do not require marking prior to counting, and are not cleared of pellets each year; thus, temporary plots are less costly and more time efficient (Freddy and Bowden 1983a, 1983b). Additionally, Freddy and Bowden (1983b) and Tucker (1991) determined that temporary plots provided similar estimates of pellet groups, and precision based on temporary plots was at least equal to precision based on permanent plots (Freddy and Bowden 1983b).

In the interest of minimizing effort to ensure that monitoring is continued in the future, I elected to conduct pellet sampling with unmarked non-permanent plots. Observers spent approximately 3.5 hours counting pellet groups in 80 plots on each pair of transects. Results from this study indicate that a minimum of 413 plots would be required to achieve the desired level of precision (detect a 20% change in population with 90% certainty) if the data could be transformed to approximate a normal distribution, and could be compared between years with a Student's *t*-test.

My data could not be adequately normalized, and will have to be compared to data from future years with the slightly less powerful, non-parametric Mann-Whitney U test. According to Hettmansperger (1984:164), the efficiency of the Mann-Whitney test never falls below 0.94 of the t-test for an underlying normal model, actually exceeds the efficiency of the t-test if the distribution deviates even slightly from normal. Assuming that the Mann-Whitney test is 0.94 as efficient as the t-test, my results indicate that a sample size of at least 438 plots would be required to achieve the desired level of precision with a Mann-Whitney U test (413 + [413 x 0.06] = 438). To be conservative, I recommend that a minimum of 1,000 plots be counted for the first few years of monitoring. Agency commitment to continue the monitoring effort at this level (12-13 pairs of transects) would be only 12-13 half "person-days". If 2 individuals counted pellets on separate transect pairs, the sampling effort could be completed in only 6 days. Because each pair of transects requires only about 3.5 hours to survey, individual pellet counters may be tempted to complete an additional pair of transects the same day. However, as Neff (1968) and Tucker (1991) strongly cautioned, boredom and observer fatigue probably affects variability significantly. I concur with Tucker's (1991) recommendation to limit each observer to $\leq$80 plots per day.

Results of the 560 pellet plots surveyed during both

years of this study, indicate a possible decline in deer numbers in the areas bisected by those pairs of transects. Although the significant decrease in number of pellet groups counted may indicate a decline in the deer population, it may merely reflect a change in deer selection of habitat between the 2 years. Severe weather and deep snowpack during winter 1990-1991 may have pushed deer off secondary habitat and forced them to become more concentrated on winter ranges than they were during the previous year, thus changing the distribution of pellet groups (Fuller 1991). In contrast to the possible decline indicated by pellet counts, the number of deer counted during roadside surveys during spring 1991 were significantly greater than the number counted in 1990. However, the large number of deer congregated in fields along roadsides suggests that these areas are preferred habitats. Results from all trend counts should be viewed cautiously until sufficient replication has been achieved. Tucker (1991) stressed the importance of conducting population indices over a number of years before forming conclusions about population trend.

Declining deer populations typically disappear from secondary habitat before the decline is noticed in more-preferred habitat (Mech and Karns 1977). It is logical, therefore, to assume that counts of pellet groups in secondary habitat should reflect population fluctuations more readily than counts of pellet groups in preferred

habitat (e.g., primary winter range). However, in years with mild winters deer may not migrate completely to winter ranges; thus, a pellet group index may indicate an increase in pellet abundance in secondary habitats. Conversely, severe winter weather may force deer to congregate densely in core wintering areas. As a result, a pellet index conducted only in secondary habitat would indicate a decline in the deer population, when in fact the deer where only distributed differently within their habitat. Consequently, it is important to conduct trend counts in both secondary and primary habitat. In my sampling scheme, only 2 pairs of transects (South5 and South6) bisected a winter range. Two other transect pairs (South1 and South2) contained very few pellet groups. I recommend eliminating these 2 pairs of transects, and replacing them with transects that bisect the white-tailed deer winter range at Starvation Ridge along the northwestern shore of Kintla Lake. To ensure that the sample is sufficient to detect a change on winter ranges, it may be advisable to add yet another pair of transects to either the Starvation Ridge or Sullivan Meadow winter range. If trend counts are standardized to sample both primary and secondary winter habitats, the index should have greater power to accurately assess whether changes in number of pellet groups indicate a change in population rather than merely a change in distribution of the deer population.

Neff (1968) and Freddy and Bowden (1983b) described

important sources of bias and error in counts of ungulate pellet groups, and Tucker (1991) described, in detail, considerations important for minimizing variability in pellet group sampling in the North Fork area. The most important sources of error include mis-counted and mis-aged groups. Neff (1968) stated that fatigue, boredom, visual acuity, and experience are the major sources of counting error, but are difficult to evaluate.

Estimation of age of pellet groups is based on subjective characteristics and is prone to error. Freddy and Bowden (1983b) and Tucker (1991) classified pellet groups as "new" or "old", whereas I classified groups into 3 categories. Because very few of my plots had "new" pellet groups, it is probably more practical to group "new" and "intermediate" aged groups together and consider them "new" as did Freddy and Bowden (1983b) and Tucker (1991). The subjective characteristics for aging pellet groups described by Freddy and Bowden (1983b) were similar to the characteristics I used, but it may be beneficial if aging characteristics were fine-tuned to specific habitats in the North Fork valley which may have different decomposition rates (e.g., dry, open meadows vs. moist, shaded forest). Freddy and Bowden (1983b:513) described establishing "aging plots" on representative microsites to aid in calibrating criteria for differentiating new and old pellet groups. Neff (1968), Freddy and Bowden (1983b), and Tucker (1991)

all emphasized that pellet counts should not be conducted when pellet groups are wet from recent rain or snow because the moisture may add a wet sheen to old pellet groups that may make them difficult to distinguish from new groups. Both the ground and pellet groups become darker as they get wet. The reduced contrast between pellet groups and the ground may result in a higher percentage of missed groups on rainy days. Avoidance of rainy periods further decreases the narrow period of time during which pellet counts can be completed. Timing of pellet counting will vary annually because of the yearly difference in date of snow melt and access to the Inside North Fork Road. In low, shaded areas, snow pack may persist into mid May and make vehicle travel to some transects impossible. Additionally, during the winter, hundred of trees typically fall over the roadway and must be cleared before the road is passable. It is also very important that pellet counts are completed before green-up when vegetation obscures pellet groups (Neff 1968, Tucker 1991). It would be difficult to standardize the sampling period between years, so future investigators must prudently evaluate results of the index between years with variability in starting dates. If snow covers the sampling area late in the season and pellet sampling is delayed, the index may reveal higher numbers of pellets simply because of the greater length of time during which pellets were being deposited.

White-tailed deer and mule deer are sympatric in this area, but in areas where transects were located, numbers of mule deer were very low. Impact of mule deer on white-tailed deer trend counts is undoubtedly inconsequential.

Population Sex- and Age- Structure

Doe:fawn and buck:doe ratios are often reported in studies of white-tailed deer ecology. Surveys are most often conducted during autumn or winter when males, females, and fawns are most easily distinguished (Downing et al. 1977). Downing et al. (1977) reported that there was rarely a period during summer or autumn when each sex and age class was equally observable; the same is likely true during winter and spring in many areas. In the North Fork area, observability of sex and age classes is probably closest to being equal during spring when deer congregate in open fields.

Surveying sex and age ratios during spring has a number of disadvantages. Fawns (short yearlings) were still, in most cases, readily discernible from adults, and many bucks were easily identified by early antler growth. However, the possibility that some bucks were indistinguishable from does because of lack of antler protrusion introduces error caused by mis-classification of sexes. Mislabeling bucks as does results in both deflated buck:doe and fawn:doe ratios. Unfortunately, I have no way of estimating my classification error rate. Another disadvantage of spring surveys, even

assuming equal observabitity of age and sex classes, and that mis-classification rates were minimal, is that spring sex and age ratios are not readily comparable to fall and winter rates most frequently reported by other authors. Sex- or age- differential mortality during winter or early spring may alter ratios significantly, but ratios should remain comparable between years.

Buck:Doe ratios estimated in this study (24-29 bucks : 100 does) were similar to ratios reported elsewhere. Nelson and Mech (1981) estimated a sex ratio of 30 bucks : 100 does in Minnesota during late winter surveys. In eastern Montana, Dusek et al. (1989) estimated a sex ratio of 25 bucks : 100 does during winter counts, and Wood et al. (1989) calculated an average ratio of 28 bucks : 100 does over a 10 year period of spring surveys.

Sex ratios are influenced by various factors, including nutrition of pregnant females (poor nutrition may skew sex ratio at birth to primarily males; a higher nutritional plane may result in a preponderance of females) (Verme 1969, 1989), sex-differential survival of fawns during summer (Hoskinson and Mech 1976, Mech and Karns 1977), sex differential hunting mortality (Roseberry and Woolf 1991), and sex differential susceptibility to predation (Kolenosky 1972; Hoskinson and Mech 1976; Mech and Karns 1977; Nelson and Mech 1986a, 1986b). Except to indicate one sex has a higher rate of mortality than another, sex ratio is not a

very useful management tool (Hayne 1984). Sex ratios should not be inferred from harvest data because does were only legal during the first 2 weeks of the 5 week season, and many hunters decline to shoot does early in the season in favor of attempting to harvest an antlered deer.

Fawn:Doe ratios estimated in this study (35-36 fawns : 100 does) were generally lower than ratios reported by other researchers. Winter and fall estimates of fawn:doe ratios do not reflect the winter mortality that influences spring ratios. Fawn:doe ratios can be affected annually by intense predation and mortality during summer (Pimlott 1967, Van Ballenberghe et al. 1975, Hoskinson and Mech 1976, Voigt et al. 1976, Mech and Karns 1977, Fritts and Mech 1981, Nelson and Mech 1986a), high winter fawn mortality (Fritts and Mech 1981, Nelson and Mech 1986b), and harsh winter weather or poor range condition that can result in low fawn production and high fawn mortality (Verme 1969). Dusek et al. (1989) reported an autumn age ratio of 85 fawns : 100 does in eastern Montana, and Wood et al. (1989) calculated an average age ratio of 66 fawns : 100 does. During a late winter survey in Minnesota, Nelson and Mech (1981) calculated a ratio of 42 fawns:100 does. I determined that fawns comprised 22-23 % of the total deer population; Fuller (1990) estimated that fawns represented 26% of a Minnesota deer population.

Fawns are typically under-represented in harvests

(McCullough 1979, Dusek et al. 1989, Roseberry and Woolf 1991:14), but there is probably little bias in age-class structure of harvested adult females (McCullough 1979). Given adequate sample size, harvest data probably yield the most reliable age-specific demographics of the population. The life table I constructed based on age structure of the 1989 and 1990 harvests yielded an average annual survival rate (68.5%) similar to the mortality rate I estimated for my radio-collared sample (70.4% - 72.5%). The large proportion of females of prime breeding age represented in the harvest during this study suggests that the herd has high resiliency to respond to annual fluctuations in mortality rates. Age structure of bucks may be mis-represented in the harvest because of differential vulnerability by age-class (McCullough 1979, but see Roseberry and Woolf 1991).

Authors frequently report age ratio estimates of a deer population and make vague inferences on the status of the population based on those age ratios (Caughley 1974). Caughley (1974) conclusively demonstrated that age ratios cannot be accurately interpreted without information on the population's rate of increase. Caughley concluded that massive increases or decreases in populations can occur without changes in age structure; or, more importantly, a dramatically increasing population may have the same age structure as a population undergoing an equally dramatic

decline.

Given the potential for mis-classification error and the difficulty in interpreting age and sex ratios, roadside surveys are probably only of value if evaluated in conjunction with reliable trend counts. If trend counts indicate a population decline and fawn:doe ratios are also low, inferences may be made concerning the problem causing the decline. Likewise, if trend counts indicate a decline, and buck:doe ratios are also low, managers should be alerted to the possibility of an over-harvest or high non-hunting mortality of bucks that could be resulting in low pregnancy rates.

CHAPTER 2

WHITE-TAILED DEER SELECTION OF FAWNING HABITAT IN AN AREA RECENTLY RECOLONIZED BY WOLVES

INTRODUCTION

An individual or group of white-tailed deer will occupy almost the same summer range each year (Leach 1982, Ozoga et al. 1982, Marchington and Hirth 1984, Krahmer 1989). In May or June, matriarchal does become solitary (Downing and McGinnes 1969, Nelson and Mech 1981) and return to the same fawning grounds they used in previous years (Ozoga et al. 1982). Retention of traditional fawning areas for family groups may enhance reproductive success during times of high population density by protecting mother-infant bond formation (Ozoga et al. 1982), and may also increase familiarity with food sources and escape routes within the home range. This familiarity with their habitat should increase survival rates of both does and their fawns (Leach 1982). Summer habitat must provide sufficient nourishment for deer, and provide cover for does and fawns during the critical fawning period when both are most susceptible to predation (Mech 1984).

Because deer fawns are so vulnerable during their first

weeks of life, predators tend to concentrate their efforts on the very young (Mech 1984). Van Ballenberghe et al. (1975) reported that deer fawns apparently became a significant food item in the diet of wolves immediately following the peak fawning period, and remained the primary prey of wolves throughout the summer. Fritts and Mech (1981) reported that fawns comprised 80% of the occurrence of deer remains in wolf scats collected in summer in Minnesota. Based on scat analyses, Nelson and Mech (1986a) also concluded that fawns were the major summer prey of wolves and suggested that wolf predation was the primary cause of fawn mortality. Wolves may limit white-tailed deer populations by preying heavily on fawns (Mech 1984; see also, Chapter 1 in this thesis).

Seasonal habitat use by deer appears to maximize access to forage and protection from the elements, and some biologists have suggested that seasonal behavior and habitat use have been strongly influenced by evolutionary predation pressure (Pimlott 1967, Hoskinson and Mech 1976, Nelson and Mech 1981). Many researchers have investigated summer habitat selection of white-tailed deer (Kohn and Mooty 1971, Slott 1980, Nelson and Mech 1981, Leach 1982, Krahmer 1989, among others), and several have described behavior of does before and during fawn-rearing (Nelson and Mech 1981, Ozoga et al. 1982, Huegel et al. 1985). However, only a few have addressed habitat characteristics of areas used during

parturition and the early fawn-rearing period (Huegel et al. 1986, Ozoga and Verme 1986, Kunkel 1992).

In areas with high predator densities, protection of critical fawning habitat may be necessary to maintain deer population size. My objective was to identify fawning areas in the area being recolonized by wolves, and attempt to identify habitat characteristics important for fawning.

STUDY AREA

This research was conducted in northwestern Montana and southeastern British Columbia in the North Fork drainage of the Flathead River. The study area extended from Camas Creek in Glacier National Park northward to 8 km beyond the Canadian border.

The North Fork valley was formed in the early Tertiary period when a gap opened behind a massive slab of Precambrian sedimentary rock that slid eastward on the Lewis Overthrust Fault (Alt and Hyndman 1973). Moraines left behind by Pleistocene glaciers resulted in the rolling topography present today (Alt and Hyndman 1973). The valley bottom varies from 4-10 km in width and rises from 1,024 m elevation in the south to 1,375 m in the northern part of the study area. Peaks of the Whitefish Range form the western border of the valley, and the Livingston Range defines the eastern border.

Land east of the North Fork of the Flathead River lies

in Glacier National Park. West of the river, land is a mosaic of Flathead National Forest, state forest, and private property. In British Columbia, land on both sides of the river is primarily under provincial ownership.

Sub-alpine fir (Abies lasiocarpa), spruce (primarily Picea engelmannii), western larch (Larix occidentalis), and Douglas-fir (Pseudotsuga menziesii) communities exist throughout the valley, but dense lodgepole pine (Pinus contorta) forests dominate most of the North Fork drainage. Abundant meadows and riparian areas are dispersed throughout the study area. Habeck (1970), Jenkins (1985), and Krahmer (1989) have provided detailed descriptions of vegetation communities in this area.

METHODS

Trapping

I trapped white-tailed deer from 15 January to 31 March 1990 and from 26 November 1990 to 26 February 1991 on 4 winter ranges in Glacier National Park within the area inhabited by wolves. Deer were trapped with modified elk-sized Clover traps (Thompson et al. 1989) or standard-sized Clover traps (Clover 1956) baited with certified noxious-weed-free alfalfa hay. When a deer was captured, I approached the trap with an assistant. Males and non-target species (e.g., mule deer) were released without being handled. Female white-tailed deer were manually restrained

and instrumented with a radio transmitter (MOD-500, Telonics, Inc., Mesa, Ariz.) with a mortality sensor (4-hr delay).

Identification of Fawning Areas

After capture, deer were located weekly. During the fawning period from late May through early July 1990-1991, I attempted to locate as many radio-collared deer as possible every day. After the fawning period, deer were again located weekly. Deer were located from the ground by triangulating at least 3 strong radio bearings, or when possible, they were located with telemetry equipment from a Cessna 180 or 182 airplane. I plotted radio bearings on USGS (1:24,000) or Energy, Mines and Resources Canada (1:50,000) topographic maps, and selected a location either at the center of the smallest triangle or polygon defined by 3 or more signal azimuths, or at the intersection of 2 such triangles. Locations were divided into 6 categories of precision (<1 ha, 1-3 ha, 3-6 ha, 6-12 ha, 12-25 ha, or >25 ha) based on size of the triangle or polygon (in 1990, only categories <12 ha, 12-25 ha, and >25 ha were recorded). To get accurate locations in June, I frequently tried to approach does on the ground until I could observe them. Because variable topography and lack of an extensive road network within the study area frequently inhibited my ability to get close-range, line-of-sight signal fixes, precise triangulations were often difficult to obtain. Only

locations with error categories of <12 ha were used to calculate habitat used for fawn-rearing. During the fawning period, I plotted daily locations and monitored day-to-day movements to determine which deer exhibited restricted movements characteristic of parturient females (Ozoga et al. 1982). After plotting locations of deer between the last week of May and the first week of July in both 1990 and 1991, I delineated an arbitrarily selected 400 m x 400 m square boundary around the densest grouping of locations to represent the border of habitat used for fawn-rearing. All locations that were taken while each deer was on its summering area and had a precision category <25 ha were used to delineate a 95% harmonic mean (25 grid cell) (McPAAL ver. 1.2, Stuwe and Blohowiak nd.) summer range.

Habitat Sampling

I divided each of 12 fawning ranges into 3 strata, and sampled habitat in 1 11.3 m-radius, circular plot randomly located in 3-4 sub-strata (of approximately equal size) within each stratum (n = 10 plots/fawning range). Using modified USFS ECODATA ecosystem classification procedures (USDA 1987), I measured or estimated habitat position, structure, and cover variables at each plot.

Position Variables.--Position variables included elevation, aspect, slope (degrees), plot position (USDA 1987), distance to nearest closed road or human trail, distance to nearest open road, distance to nearest water and

nearest running water, and distance to nearest human habitation. Distances were measured on the ground, or from topographic maps.

Structure Variables.--Structure variables included the ECODATA (USDA 1987) variables: potential natural community, structure class, and special habitat features (USDA 1987:4.42--30). In each plot I noted the presence or absence of edge, estimated hiding cover, and tabulated the number of seedlings (<2.5 cm dbh), saplings (2.5-12.4 cm dbh), poles (12.4-22.6 cm dbh), trees larger than pole-size (>22.6 cm dbh), and snags. I also recorded the number of horizontal obstructions, average height of deadfall, and the average dbh of the dominant class of overstory trees. Edge was considered present if a change in successional stage was visible from plot center. Hiding cover below 1 m and from 1-2 m above ground was estimated by averaging percent coverage of a person standing at plot center as viewed by another person standing at 30.5 m and 61 m in each of the 4 cardinal directions (Krahmer 1989). I quantified number of horizontal obstructions by counting all downed logs, <1.5 m above ground, I had to step over between plot center and 30.5 m in the 4 cardinal directions.

Cover Variables.--After noting the potential climax habitat community (Pfister et al. 1977, Lee and Pfister 1978), I divided each plot into halves. In each half, an assistant and I visually estimated canopy coverage of

graminoids, forbs, low shrubs (<15.2 cm), mid shrubs (15.2-137.2 cm), tall shrubs (>137.2 cm), and total shrub cover. Canopy coverage was also estimated for seedlings, saplings, pole-sized trees, trees larger than pole-size, total tree cover, total plant cover, and total deadfall cover. Canopy coverage for each plant form was averaged between halves and divided into ECODATA (USDA 1987) categories (Table 2.1). Canopy coverage was also estimated for the 3 most prevalent species of trees, shrubs, and forbs in each plot.

I divided 9 summer ranges (excluding fawning areas) into 3 strata and randomly sampled habitat in 1 plot in 3-4 sub-strata within each stratum (n = 10 plots/summer range exclusive of fawning range). In 3 other summering areas, I divided the range into 3 strata in which I randomly sampled 1 plot in 6-7 sub-strata within each stratum (20 plots/summer range). Habitat in summer ranges was quantified in the same manner as in fawning areas.

Analysis of Habitat Data

Continuous position variables that may have been biased by unequal sample size (i.e., elevation, slope, distances) (n = 120 plots in fawning ranges vs. n = 150 plots in summer ranges) were averaged for each deer (n = 12). I examined distributions of these variables (normal probability plots, Wilkinson 1989) and transformed variables (natural log transformation) that were not normally distributed. I then compared these variables between fawning and summer ranges

Table 2.1. Canopy cover percentages and corresponding ECODATA classification categories.

Cover %	ECODATA Category
0	0
0<x≤1	T
1<x≤5	P
5<x≤15	1
15<x≤25	2
25<x≤35	3
35<x≤45	4
45<x≤55	5
55<x≤65	6
65<x≤75	7
75<x≤85	8
85<x≤95	9
>95	F

using paired Student's t-tests.

Continuous structure variables (e.g., # seedlings, saplings, poles, larger than poles, # horizontal obstructions, deadfall height, dbh dominant overstory class, hiding cover) that probably were not influenced by un-even sample size between range types were compared between ranges with Mann-Whitney U tests ($n_1 = 120$, $n_2 = 150$). Categorical position (aspect, plot position), structure (edge, structure class, potential natural community, special features), and cover (all canopy cover estimates) variables were compared between fawn and summer ranges with Chi-square tests for homogeneity. If >20% of the category cells of a variable had <5 observations, I combined categories prior to analysis. If variables had significant Chi-square tests, I used Bonferroni z confidence intervals (Neu et al. 1974) to test category-specific observed vs. expected values. T-tests, Mann-Whitney U tests, and Chi-square tests were considered significant at $P \leq 0.10$.

I used Discriminant Function Analysis (Wilkinson 1989:540-547) to identify variables that best separated fawning areas from the remaining portion of summer ranges, and attempted to develop a model that would enable me to correctly classify habitat as being potential fawning habitat based on those selected variables. All habitat variables were entered into the full discriminant model for initial analysis. I assessed normality of all continuous

variables and transformed them if necessary prior to entering them into the model; categorical variables were entered into the model after categories were combined to reduce sparse cells (<20 % of cells contained <5 observations). Variables with high predictive value (Univariate F test ratios with P values $\leq$0.15) were entered into a reduced discriminant model. The reduced model was used to categorize plots as either belonging to fawning range or summer range based on the values of the selected variables. After calculating the percentage of correct classifications of the reduced model, I added second- and third- order interaction terms (interactions between and among continuous variables) of variables in the reduced model to attempt to improve the classification rate. Because several of the habitat position and structure variables were likely to be strongly associated (e.g., elevation, aspect, plot position, distance to water, etc.), I computed Spearman rank correlation coefficients (r_s) to evaluate relationships between variables.

Prominence values (Stringer and La Roi 1970, Krahmer 1989), which are an index of abundance and frequency of occurrence (mean cover % x $\sqrt{}$ percent frequency), were calculated by range type for all species of trees, shrubs, and forbs that were among the 3 most prevalent species of that plant form occurring in any individual plot. Prominence values of tree, shrub, and forb species in

fawning ranges were tested for association with the prominence values of the same species occurring in summer ranges. If scatter plots of prominence values between species in fawning ranges and summer ranges suggested a linear relationship, I tested association between range types with Pearson's Correlation Coefficient (r); if scatterplots indicated a non-linear relationship, I tested for association with the Spearman Ranked Correlation Coefficient (r_s) which does not require a linear relationship between variables (Walpole and Myers 1985). Strong correlation between the prominence indices of tree, shrub, and forb species in fawn ranges vs. summer ranges suggests that deer select habitat similarly in both range types irrespective of species composition. Conversely, a weak or negative correlation suggests that deer may select fawning and summer ranges differently based on a preference for or against certain species.

RESULTS

Eighty-six locations with a precision category <12 ha were used to determine 6 fawning areas in 1990. In 1991 I used 121 locations to delineate 6 more fawning ranges. Locations taken in 1991 included 56 (46.3%) with a precision category <1 ha, 40 (33.0%) in the 1-3 ha category, 21 (17.4%) in the 3-6 ha category, and 4 (3.3%) in the 6-12 ha precision category.

Fawning areas were at significantly lower elevations ($\underline{t}$ = -1.885, 11 df, $\underline{P}$ = 0.086) and were closer to water than summer ranges ($\underline{t}$ = -3.399, 11 df, $\underline{P}$ = 0.006). Slope, distances to nearest closed road or human trail, nearest open road, nearest running water, and nearest human habitation did not differ between range types ($\underline{P}$ > 0.10) (Table 2.2).

Plots in summer ranges had significantly more saplings than plots in fawning ranges (Mann-Whitney $\underline{U}$ = 7,845.5; n_1 = 120, n_2 = 150; $\underline{P}$ = 0.068), but number of seedlings, poles, trees larger than poles, snags, and number of horizontal obstructions were not different between ranges (Table 2.3). Height of deadfall and dbh of the dominant overstory class were also similar in fawning and summer ranges (Table 2.3). From 30.5 m, hiding cover between 1 and 2 m ht was significantly less in fawning ranges than in summer ranges (Mann-Whitney $\underline{U}$ = 7,830.0; n_1 = 120, n_2 = 150; $\underline{P}$ = 0.066), but differences in other hiding cover measurements were not significant (Table 2.3).

Deer selected habitat with canopy coverage of trees larger than pole size differently in fawning and summer ranges (X^2 = 13.642, 5 df, $\underline{P}$ = 0.018) (Table 2.4), but 90% family Bonferroni z confidence intervals did not detect significant differences in observed vs. expected cell values. Categorical distribution of grass cover also differed significantly between fawning and summer ranges

Table 2.2. Mean values and coefficients of variation of position variables in sample plots measured in fawning ranges and summer ranges (exclusive of fawning ranges) of 12 adult female white-tailed deer.

	Fawning Range (n=12)		Summer Range (n=12)		
Variable	$\tilde{x}$	CV	$\bar{x}$	CV	P value[1]
Elevation (m)	1203.0	0.13	1232.0	0.16	0.086
Slope (Degrees)	8.0	1.22	7.3	0.97	0.620
Dist. to nearest closed road or human trail (m)	208.0	0.59	224.0	0.50	0.517
Dist. to nearest open road (m)	331.0	0.47	343.0	0.32	0.399
Dist. to nearest water (m)	142.0	1.20	196.0	1.00	0.006
Dist. to nearest running water (m)	209.0	1.18	232.0	1.05	0.190
Dist. to nearest human habitation (m)	2775.0	1.45	2585.0	1.49	0.450

1 Probability values of 2-tailed paired t-tests.

Table 2.3. Mean values and coefficients of variation of habitat structure variables in sample plots measured in fawning ranges and summer ranges (exclusive of fawning ranges) of 12 adult female white-tailed deer.

	Fawning Range (n=120)		Summer Range (n=150)		
Variable	$\bar{x}$	CV	$\bar{x}$	CV	P value[1]
# seedlings per plot	64.1	2.55	57.2	1.58	0.591
# saplings per plot	18.7	2.74	20.6	1.14	0.068
# poles per plot	7.6	1.30	8.7	1.17	0.304
# larger than poles per plot	3.9	1.29	3.1	1.18	0.621
# snags per plot	3.5	1.57	2.9	1.61	0.384
# horizontal obstructions[2]	8.6	1.22	10.5	1.03	0.174
Deadfall height (cm)	30.5	0.52	32.0	0.57	0.458
DBH dominant overstory class (cm)	21.4	0.77	22.5	0.72	0.918
Hiding cover <1m from 30.5 m (%)	80.4	0.30	81.9	0.34	0.165
Hiding cover >1m from 30.5 m (%)	62.3	0.51	69.2	0.49	0.066
Hiding cover <1m from 61.0 m (%)	91.9	0.19	92.1	0.21	0.390
Hiding cover >1m from 61.0 m (%)	82.6	0.31	84.7	0.32	0.385

1 Probability values of 2-tailed Mann-Whitney U tests.
2 Number of horizontal obstructions <1.5m above ground encountered between plot center and 30.5 m in each of the cardinal directions.

Table 2.4. Percentage of fawn and summer range plots in each category of canopy coverage of trees larger than pole size.

Canopy Cover Category	Fawning Range (n=120)	Summer Range (n=150)
≤1%	40.00	40.00
1<x≤5%	9.17	17.33
5<x≤15%	25.00	22.00
15<x≤25%	13.33	18.00
25<x≤35%	8.33	2.00
35<x≤55%	4.17	0.67

Table 2.5. Percentage of fawn and summer range plots in each category of grass coverage.

Canopy Cover Category	Fawning Range (n=120)	Summer Range (n=150)
≤1%	15.00	18.00
1<x≤5%	27.50	18.00
5<x≤15%	20.83	17.33
15<x≤25%	8.33	9.33
25<x≤35%	3.33	8.67
35<x≤45%	5.00	5.33
45<x≤55%	0.83	1.33
55<x≤65%	6.67	3.33
65<x≤75%	2.50	6.00
75<x≤95%	4.17	10.67
>95%	5.83	2.00

(X^2 = 16.393, 10 df, P = 0.089) (Table 2.5). Observed vs. expected cell values did not differ significantly (90% family Bonferroni confidence intervals). Distributions of all other canopy cover variables did not differ significantly between range types (P > 0.10) (Table 2.6).

Aspect of fawning and summer ranges was distributed differently (X^2 = 14.585, 4 df, P = 0.006). Fawning ranges were more likely to be level or on gently rolling slopes than were summer ranges, and summer ranges were more likely to be on east-facing slopes (Table 2.7), but observed cell values did not differ significantly from expected values (90% family Bonferroni confidence intervals). An edge between successional stages of vegetation was more likely to be present on plots in fawning ranges (59.2% of plots) than in summer ranges (48.7% of plots) (X^2 = 2.953, 1 df, P = 0.086), and range types differed significantly with respect to plot position (X^2 = 18.142, 5 df, P = 0.003). Fawning ranges occurred more frequently in valley bottoms (69.2% of plots) than did summer ranges (49.3% of plots), and were less likely to occur on slopes in wide valley bottoms (11.7% of plots) than were summer ranges (31.3% of plots) (Table 2.8), but observed cell values did not differ significantly from expected values (90% family Bonferroni confidence intervals). Distribution of vegetative structural classes also differed significantly between fawning and summer ranges (X^2 = 17.770, 6 df, P = 0.007). Shrub or shrub/tree-

Table 2.6. Dominant coverage categories of cover variables measured in fawning ranges and summer ranges (exclusive of fawning ranges) of adult female white-tailed deer.

	Fawning Range (n=120)		Summer Range (n=150)			
Variable	Dominant Class (%)		Dominant Class (%)		P value[1]	df
Canopy cover-all trees	≤1%	(18.3%)	≤1%	(19.3%)	0.788	9
Canopy cover->pole size	≤1%	(40.0%)	≤1%	(40.0%)	0.018	5
Canopy cover-pole size	0	(29.2%)	5<x≤15%	(30.0%)	0.814	6
Canopy cover-sapling size	5<x≤15%	(33.3%)	5<x≤15%	(35.3%)	0.872	5
Canopy cover-seedling size	1<x≤5%	(32.5%)	1<x≤5%	(35.3%)	0.441	5
Total shrub cover	55<x≤65%	(15.0%)	35<x≤45% 65<x≤65%	(12.7%) (12.7%)	0.855	10
Tall shrub cover	0	(31.7%)	0	(28.7%)	0.900	7
Mid. shrub cover	35<x≤45	(15.8%)	15<x≤25%	(16.7%)	0.253	10
Low shrub cover	1<x≤5%	(34.2%)	5<x≤15	(28.0%)	0.601	7
Grass cover	1<x≤5%	(27.5%)	≤1% 1<x≤5%	(18.0%) (18.0%)	0.089	10
Forb cover	5<x≤15%	(15.8%)	5<x≤15% 15<x≤25%	(16.0%) (16.0%)	0.722	10
Total cover-all vegetation	>95%	(50.8%)	>95%	(60.7%)	0.130	3
Deadfall cover	5<x≤15%	(41.7%)	5<x≤15%	(38.7%)	0.487	5

1 Chi-square probability values.

Table 2.7. Percentage of fawn and summer range plots in each aspect category.

Aspect	Fawning Range (n=120)	Summer Range (n=150)
Level/ gently rolling	60.83	44.00
NW-N-NE	11.67	12.67
NE-E-SE	8.33	24.67
SE-S-SW	11.67	13.33
SW-W-NW	7.50	5.33

Table 2.8. Percentage of fawn and summer range plots in each plot position category.

Position	Fawning Range (n=120)	Summer Range (n=150)
Valley bottom	69.17	49.33
Lower slope in narrow valley bottom	6.67	3.33
Mid or upper slope in narrow valley bottom	6.67	8.67
Slope in wide valley bottom	11.67	31.33
Ridge top or knoll in wide valley bottom	5.00	6.67
Bench, terrace, or saddle	0.83	0.67

seedling and old growth structural classes occurred more frequently in fawning ranges than in summer ranges (Table 2.9), but intra-categorical differences were not significant (90% family Bonferroni confidence intervals). Deer selection of fawning and summer ranges did not differ based on distributions of potential natural communities ($\underline{P}$ = 0.425) or special habitat features ($\underline{P}$ = 0.367).

The full discriminant function model (all variables included) correctly classified 72.2% of the plots as belonging to a fawning range or summer range. Twelve variables (elevation, distance to nearest water, distance to nearest human habitation, # saplings, # trees larger than poles, hiding cover between 1-2 m ht from 30.5 m, canopy cover of trees larger than poles, edge presence, special habitat features, plot position, potential natural community, and aspect) had significant univariate F-tests ($\underline{P} \leq 0.15$) and were entered into my reduced model. The reduced discriminant model correctly classified 58.9% of the plots as fawning or summer ranges. When I added 3 second-order (elevation x distance to nearest human habitation, elevation x distance to nearest water, distance to nearest human habitation x distance to nearest water) and 1 third-order (elevation x distance to nearest human habitation x distance to nearest water) interaction term to the reduced model, all variables produced significant ($\underline{P} \leq 0.127$) univariate F tests, and the model's correct classification rate improved

Table 2.9. Percentage of fawn and summer range plots in each vegetation structural class.

Structural Class	Fawning Range (n=120)	Summer Range (n=150)
Non-vegetated or moss	1.67	2.00
Herbaceous or herbaceous/tree-seedling	7.50	8.00
Shrub or shrub/tree-seedling	30.00	21.33
Sapling	7.50	12.67
Pole/sapling	18.33	22.67
Young, mature trees	25.00	32.67
Old growth trees	10.00	0.67

only to 60.4%.

Slope, aspect, plot position, # of saplings, and all hiding cover measurements were strongly associated (r_s = 0.49-0.65) with elevation (Table 2.10). As expected, aspect, plot position, and slope were all closely correlated (r_s = 0.62-0.87) (Table 2.10). All hiding cover measurements were strongly associated with number of saplings per plot (r_s = 0.46-0.59) (Table 2.10). Distance to nearest water was only moderately correlated with the other variables ($r_s \leq 0.26$) (Table 2.10).

Prominence values of dominant tree species (Table 2.11) in fawning ranges were strongly associated ($r = 0.917$, $P < 0.001$) with prominence values of dominant tree species in summer ranges. Prominence values of dominant shrub species (Table 2.12) were also strongly correlated between range types ($r_s = 0.711$, $P < 0.001$), but prominence values of dominant forb species (Tables 2.13) were not as strongly correlated ($r_s = 0.484$, $P < 0.001$) between range types. Although heartleaf arnica (Arnica cordifolia) and lady fern (Athyrium felix-femina) were more prevalent in summer ranges than in fawning ranges, fireweed (Epilobium angustifolium) was substantially more abundant in fawning areas (2.13).

DISCUSSION

Predation probably plays an important role in the habitat selection of white-tailed deer. In areas with high

Table 2.10. Spearman Rank (r_s) correlation matrix[1] of selected habitat position and structure variables measured on 270 plots in 12 female white-tailed deer summer ranges (including fawning areas).

Variable	Elev	Slope°	Aspect	Plot Posn	Dist Watr	# Seedl	# Sapl	# Pole	# >Pole	Hiding Cover 30m <1m	Hiding Cover 30m 1-2m	Hiding Cover 61m <1m	Hiding Cover 61m 1-2m
Elevation	1.00												
Slope°	0.65	1.00											
Aspect	0.51	0.87	1.00										
Plot Position	0.49	0.65	0.62	1.00									
Dist. to water	0.17	0.22	0.21	0.26	1.00								
# Seedlings	0.34	0.35	0.30	0.38	0.17	1.00							
# Saplings	0.55	0.40	0.36	0.40	0.17	0.68	1.00						
# Poles	0.38	0.34	0.31	0.26	0.12	0.37	0.69	1.00					
# > Pole-size	0.15	0.17	0.24	0.10	-0.06	0.13	0.34	0.63	1.00				
Hiding Cover													
30m <1 m	0.54	0.35	0.32	0.34	-0.01	0.30	0.46	0.34	0.31	1.00			
30m 1-2 m	0.56	0.40	0.36	0.38	0.04	0.37	0.56	0.46	0.38	0.87	1.00		
61m <1 m	0.45	0.37	0.34	0.34	0.00	0.40	0.48	0.43	0.41	0.76	0.72	1.00	
61m 1-2 m	0.56	0.46	0.41	0.41	0.01	0.45	0.59	0.48	0.42	0.76	0.80	0.83	1.00

1 Correlation coefficients can be tested for significance by computing $z = r_s \sqrt{(n - 1)}$ and comparing with critical values of the standard normal distribution (Walpole and Myers 1985). For sample size n = 270, correlations are significant at $P \leq 0.05$ if $r_s \geq 0.10$.

Table 2.11. Prominence values[1] of dominant tree species in vegetation plots in white-tailed deer fawning and summer ranges.

Species	Fawning Range	Summer Range
Abies lasiocarpa	95.7	91.0
Larix occidentalis	59.8	60.4
Pinus contorta	82.9	73.2
Picea spp.	137.4	127.1
Pinus ponderosa	3.4	8.0
Populus trichocarpa	28.3	33.7
Populus tremuloides	61.5	21.7
Pseudotsuga menziesii	64.3	99.4
Salix spp.	2.7	0.0
Thuja plicata	0.0	0.8

1 Prominence value = mean canopy cover % x $\sqrt{}$ frequency of occurrence %.

Table 2.12. Prominence values[1] of dominant shrub species in vegetation plots in white-tailed deer fawning and summer ranges.

Species	Fawning Range	Summer Range
Acer glabrum	12.0	29.7
Alnus spp.	105.6	141.7
Amelanchier alnifolia	66.4	41.6
Artemisia tridentata	0.0	30.2
Arctostaphylus uva-ursi	37.5	32.2
Berberis repens	18.4	25.9
Chimaphila umbellata	0.0	7.7
Cornus canadensis	35.3	49.8
Cornus stolonifera	68.8	42.4
Crataegus douglasii	3.4	7.7
Ledum glandulosum	8.9	0.0
Linnaea borealis	70.8	63.0
Lonicera involucrata	35.3	31.5
Lonicera utahensis	1.4	13.0
Menziesia ferruginea	32.0	65.3
Oplopanax horridum	32.6	8.4
Pachistima myrsinites	42.9	42.5
Potentilla fruiticosa	2.3	6.0
Populus trichocarpa	35.8	10.8
Populus tremuloides	13.1	11.4
Prunus virginiana	8.4	0.4
Rhamnus alnifolia	85.1	28.8
Ribes spp.	23.5	0.0
Rosa spp.	30.2	21.7
Rubus idaeus	0.0	25.7
Rubus parviflorus	60.5	108.3
Salix spp.	49.3	74.7
Sambucus racemosa	2.7	0.0
Shepherdia canadensis	91.0	118.9
Spiraea betulifolia	43.5	48.5
Symphoricarpos albus	167.2	118.4
Tsuga mertensiana	0.0	28.8
Vaccinium caespitosum	25.8	32.0
Vaccinium globulare	30.9	87.1
Vaccinium scoparium	17.9	32.6

1 Prominence value = mean canopy cover % x $\sqrt{}$ frequency of occurrence %.

Table 2.13. Prominence values[1] of dominant forb species in vegetation plots in white-tailed deer fawning and summer ranges.

Species	Fawning Range	Summer Range
Achillea millefolium	13.4	11.0
Actaea rubra	2.7	2.5
Anaphalis fruiticosa	0.8	2.0
Anaphalis margaritacea	9.8	3.1
Antennaria racemosa	2.1	0.0
Apocynum androsaemifolium	2.7	0.0
Aralia nudicaulis	14.7	24.3
Arnica cordifolia	77.8	124.2
Aster spp.	42.4	56.3
Athyrium felix-femina	0.0	78.2
Castilleja miniata	2.7	0.6
Campanula rotundifolia	2.3	0.0
Chrysopsis villosa	0.4	0.4
Cirsium arvense	2.7	7.1
Cirsium sp.	8.9	2.5
Clintonia uniflora	20.9	32.2
Cryptogramma crispa	0.0	0.4
Epilobium angustifolium	157.3	94.5
Equisetum arvense	113.9	134.6
Fragaria spp.	47.1	59.6
Galium boreale	9.6	10.9
Galium triflorum	4.7	12.2
Geranium viscosissimum	20.9	15.2
Goodyera oblongifolia	0.4	0.0
Hedysarum spp.	2.7	10.8
Heracleum lanatum	11.9	2.5
Mentha spp.	2.7	2.9
Perideridia gairdneri	22.7	8.4
Plantago sp.	0.0	0.6
Polygonium amphibium	0.0	16.7
Potentilla sp.	0.7	2.5
Pteridium aquilinum	2.7	6.4
Senecio fremontii	12.1	0.0
Senecio triangularis	2.7	3.4
Smilacina stellata	7.9	12.3
Solidago sp.	32.0	10.1
Streptopus amplexifolium	22.3	2.5
Taraxacum sp.	21.1	0.4
Thalictrum occidentale	23.2	39.6
Trifolium spp.	0.4	23.8
Urtica dioica	44.7	2.5
Vicia sp.	8.9	0.0
Verbascum thapsus	0.4	0.0
Veratrum virides	0.0	8.4
Viola spp.	24.6	41.8
Xerophyllum tenax	2.7	2.0

1 Prominence value = mean canopy cover % x $\sqrt{}$ frequency of occurrence %.

predator densities, fawns suffer high predator-related mortality, especially during the first month after birth (Dood 1978, Ozoga and Verme 1986, Kunkel 1992). Dood (1978) reported 32-36% mortality of mule deer fawns in northcentral Montana, where coyotes are the major predator of deer. Ozoga and Verme (1986) reported a 32% loss of neonatal white-tailed deer when black bears were present on their study area, compared to only 10% mortality when bears were absent. In northeastern Minnesota, Kunkel (1992) reported a 52% mortality rate for newborn fawns where wolves were responsible for 56% of the deaths and black bears were implicated in the remaining 44%. Given the impact predators may have on ungulate production, it follows that evolutionary pressures should favor does that select habitat that decreases vulnerability of fawns to predation during parturition and the following month.

Although actual bedsites are chosen by the fawn, the general habitat surrounding the bedsites are strongly influenced by the mother (Huegel et al. 1986). Ozoga and Verme (1986) indicated that a neonate's bedsite habitat, movement patterns, and evasive tactics when threatened by a predator are largely maternally controlled, and that a doe's fawn-rearing skill, and thus survival of her fawns, improves with experience. Mature does typically nurse fawns in dense cover and avoid openings (Ozoga and Verme 1986). Dood (1978), Huegel et al. (1986), and Kunkel (1992) all reported

that fawn bedsites had a greater density of vegetation than surrounding sites. Conversely, in my study, measurements of hiding cover <1 m above ground did not differ between fawning and summer ranges, but at a distance of 30.5 m, plots in fawning areas had less hiding cover at 1-2 m height than summer range plots. It may not, however, be appropriate to compare deer selection of fawning sites between studies conducted in different habitats. Deer in my study may have had more sufficiently dense habitat to choose from than did deer Dood (1978) studied in northcentral Montana or deer studied by Huegel et al. (1986) in Iowa. Additionally, habitat in the fawning areas I quantified in my study may not be correlated directly to bedsites selected by fawns. I speculate that selection of fawning habitat in areas with less cover between 1-2 m height may permit mothers an increased ability to see predators in vicinity of fawn bedsites, without necessarily compromising the security of bedded fawns. Experienced does may distract predators from fawns by leading them away from bedsites, or they may defend the fawns if necessary (Ozoga and Verme 1986). Ability of does to detect predators may also have influenced the presence of edge in fawning areas. In my study, edges occurred more frequently in fawning areas than in summer ranges, and may act to improve fawn survival by permitting does to detect and distract predators.

Huegel et al. (1986) suggested that ambient temperature

was an important factor influencing fawn selection of bedsites, and that choice of aspect was a function of temperature. On cool days, fawns bedded on slopes facing the sun, whereas on warm days, they selected beds on slopes facing away from the sun (Huegel et al. 1986). Fawn bedding areas in Iowa also had greater tree canopy cover than surrounding habitat. Although canopy cover of trees pole-size and smaller did not differ between range types in my study, fawning ranges tended to have more canopy cover of trees larger than poles than did summer ranges. Shade produced by tree cover likely results in lower temperature and may be a factor involved with doe and fawn selection of habitat with greater tree canopy.

Temperature may also have a strong influence on other habitat position features does select for fawning ranges. Fawning ranges in my study occurred at significantly lower elevations than summer ranges, occurred more frequently on level ground or gently rolling slopes, and were more likely to be located in valley bottoms. Elevation, aspect (level ground), and plot position (valley bottoms) were strongly related. Low elevation valley-bottoms in the North Fork area are the areas most likely to contain dense hiding cover and have greater tree canopy cover, and thus, have greater protection from predators, and may also have thermoregulatory advantages for parturient females and fawns.

Although my results indicated only a moderate correlation between distance to water and the other variables, low elevation valley-bottoms and level habitats are areas that, at least intuitively, are more likely to have water. Fawning ranges in my study were closer to water than summer ranges. Several authors observed a preference for riparian areas in deer summer ranges (Hoskinson and Mech 1976, Slott 1980, Leach 1982, Compton et al. 1988, Krahmer 1989). In fact, Hoskinson and Mech (1976) reported that >80% of deer summer ranges were bordered on at least 1 side by a major waterway. Riparian areas provide a diversity of forage species, but also may act as escape refugia from predators (Mech 1970, Hoskinson and Mech 1976). In addition to serving as an anti-predator strategy, presence of water may be of more importance in fawning areas than in summer ranges. Does may select fawning areas near water to enable them to replace water lost to milk production and the metabolic stress of lactation. However, according to Moen (1973), milk production increases until it peaks when fawns reach 10-15 kg body weight 20-40 days into lactation. After fawns are about a month old and are more mobile, does may be willing to travel farther to water.

Although univariate tests revealed significant differences of several variables between range types, my full discriminant model only correctly classified 72.2% of the plots as belonging to either a fawning or summer range,

and the reduced model (12 variables) classified only 58.9% of the plots correctly. The poor classification rate of my discriminant models suggests that the variables I measured were insufficient to completely distinguish between range types. Several factors may be responsible for the inadequacy of my models: 1) deer may not select fawning habitat based on vegetative or position characteristics that are specifically chosen for the purpose of fawning; 2) deer may have selected habitat based on variables other than those I measured; 3) fawning areas may have been different from summering areas, but were not a limiting factor within summer ranges (i.e., other sites in summer ranges may have been of equal quality but were not used for fawning); 4) sample size may have been insufficient to adequately represent habitat within fawning and summer ranges; 5) ocular cover estimates and ECODATA categorical classification may have been too imprecise for microhabitat comparisons; 6) does may have separated themselves far enough away from their fawns that telemetry locations of adults did not represent habitat used by fawns following parturition; 7) precision of my telemetry locations may have been insufficient for the level of microhabitat analysis necessary to distinguish between fawning ranges and the remainder of the summer range; 8) because of the great variability of habitat used by deer, the discriminant model may have been unable to identify threshold values necessary

to differentiate between range types selected by different deer across a large area in a heterogeneous environment. Furthermore, because several of the measured habitat variables were closely associated to one another, their inclusion in the discriminant model likely added little to the model's predictive value.

Because the majority of the telemetry locations I used to determine fawning ranges had precision polygons <6 ha (96.7% in 1991), and I frequently checked accuracy of my triangulations by verifying locations by observing the radio-collared deer, my location data were probably adequate for habitat analysis. In addition, Ozoga and Verme (1986) calculated average distances between radio-collared whitetail does and their radio-collared fawns, and determined that does typically stayed within 150 m of their bedded fawns. Riley and Dood (1984) estimated that mule deer does were <250 m away from their bedded fawns during 76% of their telemetry locations. If does were within 150 m of their fawns during most of my June telemetry locations, the arbitrary 400m x 400m area I used to delineate fawning areas should have encompassed the sites used by fawns.

Huegel et al. (1986) concluded that plant species found at fawn bedsites are probably unimportant except for their value as concealment cover. High positive correlations between prominence values of tree and shrub species in fawning and summer ranges in my study lend support to their

conclusion. Although prominence values of forb species were only moderately associated between range types, differences in prevalence of species may have been related more to different habitat associations (elevation, aspect, potential natural community, etc.) in fawning and summer ranges than to deer selection of habitat based on specific species. However, fireweed, which was substantially more abundant in fawning ranges, may have been selected as a preferred forage species, as well as for its excellent cover value.

Regardless of my inability to develop a useful predictive discriminant function model to identify potential fawning areas within deer habitat, there is little doubt that vegetative structure of fawning areas and fawn bedsites influences fawn survival. It may be difficult or impossible to identify threshold values for specific habitat features that determine if deer would select that habitat for fawning. Deer occur throughout the North Fork valley during the summer, and habitat within their summer ranges encompasses a wide range of variability. Deer may select specific qualities of habitat within their ranges for fawning, but because of the enormous variance in range composition between individual deer, it is unlikely that a multivariate model will be able to adequately delineate thresholds necessary to classify habitat as being a potential fawning area with an acceptable level of confidence. Rather than attempting to predict range type

based on the spectrum of habitat used by all deer, it may be more beneficial to rely on results of univariate tests and focus on with-in range selection of individual deer. In addition, intensive vegetation description of actual fawn bedding areas, or at random points within the ranges occupied by fawns (rather than the parturient and post-parturient does), would probably be more likely to reveal particular habitat features deer select during the period newborn fawns are most susceptible to predation. If an adequate sample size could be obtained, a comparison between habitat selected by does of fawns that survived vs. habitat selected by does of fawns that were killed by predators might reveal valuable information that may be important for protecting critical habitat in areas with high predator densities.

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APPENDIX A

PROCEDURES AND RECOMMENDATIONS FOR HANDLING WHITE-TAILED DEER IN NON-COLLAPSIBLE CLOVER TRAPS

Use of Clover traps (Clover 1956) is one of the most common methods for capturing deer, but it is also one of the most stressful capture techniques (Delgiudice et al. 1990). When possible, collapsible Clover traps should be used to minimize the possibility of injury to both deer and researchers. Use of an anesthetic (e.g., xylazine hydrochloride and ketamine hydrochloride) probably greatly reduces stress to deer during prolonged handling, and may allow the researcher to process the animal more efficiently. However, in some instances researchers may not have access to collapsible traps, or may be otherwise required to use non-collapsible traps without the aid of chemical restraint. I am aware of few detailed descriptions or recommendations for handling deer captured in non-collapsible traps (but see Rongstad and McCabe 1984), and think it may be beneficial to others if I document procedures I found to be most effective and safest for both deer and handlers.

Trap Size and Placement

Large Clover traps, such as those used to capture elk (Thompson et al. 1989), should not be used for capturing deer unless absolutely necessary. Deer have much more room to move around in larger traps and have greater momentum

when they run into the netting or trap frame while attempting to escape; thus, they are more likely to be injured (broken necks are commonly reported by researchers who have trapped deer with large Clover traps). In addition, because deer have greater mobility in larger traps, there is a greater chance of injury to researchers attempting to restrain the deer.

Traps should always be placed far enough from a road or trail that trapped animals will not be able to see or hear people passing by. Trapped deer invariably become frantic when they become aware of the presence of people; in addition to increasing stress on deer, the possibility of injury is greatly increased.

Recommendations for Handling Trapped Deer

Before approaching a trap to check for captured deer, technicians should organize equipment necessary for processing the animal (e.g., radio collar, data forms, blindfold, ropes, injections, etc.). At least 2, but no more than 3, technicians should quietly approach the trap. When the captured deer begin to react excitedly, the technicians should rush to the trap as quickly as possible. If deer-sized Clover traps are used, the "assistant" should raise the door and attach it to the top of the trap, while the "handler" moves into the trap to grab the deer. If possible, the handler should grab the deer's hind legs and pull them out to the assistant. By extending the deer's

hind legs as far back as possible, technicians will be better able to restrain the deer from kicking. The handler should then push the deer down on its side so that its chest and legs face away from him. Once the deer is on its side, the assistant outside the trap should tie the deer's hind legs together. It is important that the hind legs are tied tightly above the hock joint, or the deer will inevitably loosen the rope and free both legs. After the hind legs are tied together, they should be secured tightly to the bottom of the trap frame to prevent the deer from kicking. After the deer is down and restrained from kicking, 1 technician maintains pressure on the deer's neck and shoulder area, but should be careful to avoid putting weight over the rib cage or abdomen. Weight on these areas may restrict breathing; if the rumen is pushed into the diaphragm, the deer may suffocate. One technician should be assigned to monitor the deer's breathing and ensure that its airway is not obstructed (i.e., make sure nose and mouth are up). Technicians should blindfold the deer as soon as possible after restraint. Deer often react violently when their eyes are first covered, but this behavior is usually short-lived. The blindfold will protect the deer's eyes from damage, and, by blocking vision, will probably reduce the stress the deer will experience during handling. After the radio collar is fitted and necessary data have been collected, the blindfold should be removed and the deer's legs should be untied from

the trap (the deer's legs remain tied together). While the deer's hind legs are still tied together and extended, technicians should try to slowly pull the deer out of the trap. After the deer is removed from the trap, technicians should untie the hind legs and release the deer in a direction free of obstacles. If it is not possible to remove a deer from the trap prior to release because of the size, strength, or belligerent disposition of the animal, both technicians should exit the trap and quickly move around behind it so the deer will be frightened toward the open door. When released, deer usually respond by frantically trying to escape their captors. Consequently, it is preferable to remove deer from the trap prior to release because it greatly reduces potential for injury that may be caused if the deer hits its head on the metal trap frame while trying to escape.

Procedures for handling deer in large Clover traps are similar to procedures for standard size traps, but when large traps are used, both technicians should enter the trap quickly and shut the door behind them. After 1 of the technicians grabs the deer, the other grabs and extends the hind legs and secures them to the trap frame. Researchers should not attempt to manually restrain antlered deer in large Clover traps.

All capture techniques are highly stressful to deer, and some mortalities are likely to occur if large numbers of

deer are captured. By doing as much as possible to minimize stress to deer (e.g., being quiet throughout the handling procedure, being organized and efficient, etc.), researchers can minimize trap-related stress, injuries and mortalities.

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APPENDIX B

PROCEDURES FOR MINIMIZING PREDATOR/HUMAN CONFLICTS WHILE INVESTIGATING UNGULATE MORTALITY IN THE NORTH FORK DRAINAGE OF THE FLATHEAD RIVER

Note: I proposed the following procedures for investigating ungulate mortalities prior to beginning fieldwork on my thesis research. I followed these procedures during all mortality investigations during the study, and experienced no confrontations with predators. Adherence to these methods does not, however, guarantee the safety of others investigating mortalities in areas populated by bears and/or mountain lions.

INTRODUCTION

Accurate estimates of mortality rates are critical to understanding the dynamics of ungulate populations. Cause-specific mortality rates are particularly important if research objectives concern an evaluation of the impacts individual sources of mortality may have on a population. In many areas, the public is concerned about the influence of predators on big game animals. To gain information on cause-specific mortality affecting ungulate populations, researchers often rely on motion-sensitive radio-collars (mortality collars) to enable them to detect and investigate ungulate morality. Because it may be impossible to identify an exact cause of death of a carcass that has been scavenged, it is critical to investigate all incidences of mortality as soon after the time of death as possible. However, in areas inhabited by bears (Ursus spp.), mortality investigations could be extremely dangerous and potentially

life-threatening to researchers. Similarly, it is apparent that in recent years confrontations between mountain lions (Felis concolor) and humans have increased substantially (Beier 1991).

Both black bears (U. americanus) and grizzly bears (U. arctos) are effective predators and scavengers. A grizzly bear may aggressively defend its food source against any animal it thinks may be competing with it for food (Herrero 1985). To avoid having a carcass scavenged, grizzlies sometimes cover a carcass with vegetation, branches, and dirt, and sleep on top of it or nearby (Herrero 1985, Larsen et al. 1989). Encounters between humans and bears that are near or feeding on a carcass are considered to be among the most dangerous human/bear interactions (Herrero 1985:31-38).

I recognize the potential danger of investigating mortality of ungulates in an area densely populated by mountain lions, and both black and grizzly bears. It is, however, critical to my research objectives that I investigate each incidence of mortality as quickly as possible. During my study of mortality of white-tailed deer in the North Fork of the Flathead River drainage, I will adhere to the following protocol to minimize the possibility for human/predator conflict, while maximizing the safety of both investigators and predators.

PROCEDURE

Investigation crew

All cases of mortality will be examined in the field by a group of 3. One member, the "investigator," will be responsible for locating the carcass (via radio telemetry) and identifying cause of death. Another member will be armed with a 12-gauge semi-automatic or pump-action shotgun loaded with slugs. This individual will be responsible for watching for bears and protecting the group from an attack. It will be the duty of the third group member to record data reported by the investigator. The "data-recorder" will also help watch for bears and be responsible for radio communication to a fourth member located at a designated base station.

The armed member will have completed the National Park Service Firearms Training Course and the Bear Management Training Course prior to carrying firearms within Glacier National Park. Under no circumstances will shots be fired unless an attack is underway.

Approach

Upon receiving a mortality signal, the investigator will locate the animal as accurately as possible by triangulation from the road. At this time, the investigator will scan frequencies of all radio-collared predators (bears and wolves [and, in the future, mountain lions]) to determine if any are in the immediate vicinity of the

carcass. If a radio-collared bear is present, the investigation will be postponed until the predator leaves the area.

After determining the general location of the carcass, the field crew will examine topographic maps and plan the safest approach. If the carcass is within Glacier National Park boundaries, the appropriate sub-district ranger will be notified. When possible, the carcass will be approached from the upwind, most open, and highest-ground direction so predators in the direction of the carcass will be more likely to detect the researchers and less likely to be surprised.

Before approaching on the ground, the field crew will establish radio contact with a fourth member at a designated base station. Radio contact will be maintained at 10-minute intervals throughout the investigation until the ground crew has returned from the field.

The ground crew will travel close together and in single-file at all times. The armed crew member will lead and be followed by the investigator (radio-tracker), and the data recorder. During the approach, the ground crew will whistle, yell, and talk loudly among themselves. The crew will stop every 5 minutes (at least every 2 minutes when within 500 m of carcass) to look and listen carefully, and sound a compressed-air horn for 5 seconds before continuing. When within 100 m, the group will continually make noise and

look and listen for bears and mountain lions. The crew will attempt to find bear sign (scats, tracks, broken vegetation). If a bear or fresh bear sign is present, the crew will immediately leave the area.

Upon reaching the carcass, the data recorder and the member armed with the shotgun will select spots close to the carcass that will allow the greatest vantage point. If possible, the armed member should be on higher ground and perpendicular to the shortest distance between the carcass and the densest cover. Before continuing, all members will locate the nearest tree climbable to a height >10 m (Herrero 1985). If a bear is seen or there is evidence of one having been there, the crew will leave for at least 3 days.

Examination

While the investigator examines the carcass and describes the remains and kill pattern (if a predator kill), the data-recorder will record data, continue to make radio contact with the designated base station, and sound the air horn at 2-minute intervals. The armed crew member will constantly watch and listen for bears.

Departure

After the examination is completed, the ground crew will depart the scene in the same manner as they approached. The group will continue to make noise and maintain radio contact with the base station until they return to their vehicle or the base station.

Statement of Intent

It is my intention to gain as much information as possible about mortality of deer, elk, and moose in the North Fork drainage of the Flathead River, but, at the same time, avoid conflict with all predatory species. While investigating ungulate mortality, I will take all precautions to avoid aggressive interactions with bears. However, because of the potential danger, I feel it is necessary for at least one member of the crew to carry a firearm to ensure the safety of the group. Firearms would be used only for protection during an attack that may develop in spite of our precautions.

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APPENDIX C

Radio frequency (MHz), date and location of capture, and age of female white-tailed deer when captured, 1990-1991.

ID#	Frequency	Date	Location	Age[1]
101	148.790	01/23/90	Kintla Lake, GNP[2]	6.5
102	148.810	01/30/90	Kintla Lake, GNP	7.5
103	148.820	01/21/90	Kintla Lake, GNP	2.5
104	148.830	02/22/90	Kintla Lake, GNP	*1.5
105	148.840	03/24/90	Kintla Lake, GNP	7.5
106	148.850	03/23/90	Kintla Lake, GNP	13.5
107	148.860	03/24/90	Kintla Lake, GNP	4.5
108	148.870	01/30/90	Kintla Lake, GNP	1.5
109	148.880	03/20/90	Kintla Lake, GNP	5.5
110	149.030	03/03/90	Polebridge, GNP	0.5
111	148.900	02/03/90	Sullivan Meadow, GNP	1.5
112	148.920	02/01/90	Sullivan Meadow, GNP	unk[3]
113	148.930	02/04/90	Sullivan Meadow, GNP	6.5
114	148.940	02/04/90	Sullivan Meadow, GNP	2.5
115	148.950	02/03/90	Sullivan Meadow, GNP	6.5
116	148.960	02/05/90	Sullivan Meadow, GNP	2.5
117	148.970	02/01/90	Sullivan Meadow, GNP	9.5
118	148.980	02/02/90	Sullivan Meadow, GNP	*1.5
119	148.990	03/07/90	Sullivan Meadow, GNP	4.5
120	149.000	01/30/90	Sullivan Meadow, GNP	13.5
121	149.010	03/07/90	Sullivan Meadow, GNP	*2.5
122	149.020	03/08/90	Sullivan Meadow, GNP	2.5
123	149.020	03/31/90	Sullivan Meadow, GNP	7.5
124	149.050	11/29/90	Bowman Rd., GNP	1.5
125	149.060	12/03/90	Bowman Rd., GNP	2.5
126	148.840	12/04/90	Polebridge, GNP	1.5
127	148.850	12/05/90	2 km S. Kintla Cr.,Pvt[4]	8.5
128	148.890	12/12/90	2 km S. Kintla Cr., Pvt	5.5
129	149.070	12/14/90	Polebridge, GNP	1.5
130	149.090	12/20/90	Bowman Rd., GNP	4.5
131	149.080	01/09/91	Kintla Cr./N. Fork, FNF[5]	0.5
132	148.970	01/09/91	2 km S. Kintla Cr., Pvt	5.5
133	149.110	01/12/91	Kintla Cr./N. Fork, FNF	1.5
134	149.100	01/15/91	Kintla Cr./N. Fork, FNF	9.5
135	148.880	01/21/91	2 km S. Kintla Cr., Pvt	0.5
136	149.090	02/04/91	Ford Work Center, FNF	3.5
137	148.890	02/22/91	Kintla Cr./N. Fork, FNF	10.5
138	148.880	02/23/91	Kintla Cr./N. Fork, FNF	2.5

1 Age estimates marked with an asterisk are based tooth wear and/or size of the deer. All other age estimates are based on cementum analysis.
2 GNP = Glacier National Park.
3 unk = Unknown - no estimate.
4 Pvt = Private Property.
5 FNF = Flathead National Forest